# Cyst Shell Morphology of the Fairy Shrimps (Crustacea: Anostraca) of Australia

Brian V. Timms[1], William D. Shepard[2] and Richard. E. Hill[3]

[1] School of Environmental and Life Sciences, University of Newcastle, Callaghan NSW 2308.
[2] Department of Biology, California State University, Sacramento California 95819, USA.
[3] 3900 Central Avenue, Fair Oaks California 95628, USA.

Timms, B.V., Shepard, W.D. and Hill, R.E. (2004). Cyst shell morphology of the fairy shrimps (Crustacea: Anostraca) of Australia. *Proceedings of the Linnean Society of New South Wales* **125**, 73-95.

Cyst shell morphology is described for 31 species and 4 genera of endemic Australian fairy shrimp. All four genera have distinctive cyst shell structure.

Manuscript received 3 May 2003, accepted for publication 23 July 2003.

KEYWORDS: *Branchinella*, branchiopodid, *Parartemia*, *Streptocephalus*.

## INTRODUCTION

Australia has a relatively simple fauna of anostracans, with about 50 species in five genera. The list is currently growing because of recent discoveries, but presently stands at 29 described and one undescribed species of *Branchinella* (Thamnocephalidae), 8 described and 7 undescribed species of *Parartemia* (Parartemidae), two species of *Artemia* (Artemidae), and two described and perhaps many undescribed species of *Streptocephalus* (Streptocephalidae) and a species of an undescribed branchipodid genus (Timms, in press). All species are endemic, except for the two species of *Artemia*, one of which is certainly introduced and the other possibly introduced (see McMasters et al., in press; Timms, in press).

Little is known on the biology of Australian species (Timms, in press) and even less on detailed morphology and of adults and of cysts. Some general observations on cyst morphology of some species have been made by Herbert and Timms (2000), Timms (2002) and Timms and Geddes (2003).

Cyst shell morphology is much better known in fairy shrimp that occur in Europe, Africa and North America, and even the species occurring on some oceanic islands have been described. Political units from which cysts of fairy shrimp have been described include: France (Thiéry and Gasc 1991); Italy (Mura 1986, 1991b); California (Hill and Shepard 1997, Shepard and Hill 2001); Africa (Brendonck and Coomans 1994a, b; Brendonck and Riddoch 1997); and the Galapagos Islands of Ecuador (Brendonck et al. 1990). Some cyst studies have centered on certain families, genera, subgenera or species groups: streptocephalids and thamnocephalids (Mura 1992, DeWalsche et al. 1991); streptocephalids (Hamer et al. 1994a, b); *Branchinecta* (Mura 1991a), *Chirocephalus* (Mura 2001, Mura et al. 2002), *Linderiella* (Thiéry and Chanpeau 1988); *Streptocephalus* (Brendonck et al. 1992; Brendonck and Coomans 1994a, b; *Streptocephalus (Parastreptocephalus)* (Brendonck et al. 1992); the *Streptocephalus sealii* group (Shepard 1999). Cyst descriptions are also now becoming a common part of descriptions of new species. Identification keys based solely on cyst morphology have been produced for some branchiopod groups (Brendonck and Coomans 1994a, b; Shepard and Hill 2001; Thiéry and Gasc 1991). Cyst shell morphology is useful for identifying all genera so far examined, and many, but not all, species. Besides a perceived lack of differences between some related species, intraspecific variation associated with various predation levels (Mura et al. 2002, Dumont et al. 2002) and perhaps incipient speciation (Mura et al. 2002) may lead to confusion in some species.

Cyst morphology includes both external and internal structure (Hill and Shepard 1997). The outermost part of the shell is represented by the cortex surface. This surface often has spines, spinules, ridges of several different forms, buttons and ropey folds. The cortex is generally relatively thin. Below the cortex is the thick alveolar layer, which may be divided into various distinct sublayers. The alveolar layer is usually highly vacuolated with the vacuoles separated by curved or straight, solid struts of varying length. The innermost layer is the tertiary base which is relatively thin, solid and sometimes lamellate throughout. Often the interior surface has an impressed polygonal pattern. An additional cyst shell character is inpocketing of the entire shell. Inpocketing is only typical of cyst shells which have a fairly uniform alveolar layer.

The goal of this paper is to describe the external and internal structure of the cyst shell in as many as possible of the endemic Australian fairy shrimp fauna. This is a prerequisite for understanding differences between genera and species, as a base for understanding any intraspecific differences and for the construction of identification keys. Comparative information on *Artemia* cysts is provided by Shepard and Hill (2001) and is not repeated here. This is of overseas material, but is unlikely to be different from Australian cysts, as all *Artemia* cysts are the same (G. Mura, pers. com.; W. Shepard, pers. com.), except for *A. monica*, which does not occur here.

## METHODS

Specimens of fairy shrimps were collected in the field and preserved in 70-80% ethyl alcohol and identified by BVT using Geddes 1981 and Timms in press. Females with the most mature looking cysts (those with a regular pattern all over the surface and which retain their sphericity) present in the brood pouch(es) were selected for dissection of the cysts. Cysts were removed and air-dried on filter paper. Then the cysts were mounted on SEM stubs using double-stick tape and gold-coated. A Zeiss DSM 940 SEM was used for measuring and photographing the cysts. Cyst morphology is described as in Hill and Shepard (1997), Shepard (1999) and Shepard and Hill (2001). Cyst stubbs have been stored in the private collection of REH.

## RESULTS

Cysts were obtained for 31 of the 50 or so species of fairy shrimp known to exist in Australia. Those species include: *Branchinella affinis* Linder 1941, *B. arborea* Geddes 1981, *B. australiensis* (Richters 1876), *B. basipina* Geddes 1981, *B. buchananensis* Geddes 1981, *B. budjiti* Timms 2001, *B. campbelli* Timms 2001, *B. complexidigitata* Timms 2002, *B. dubia* (Schwartz 1917), *B. frondosa* Henry 1924, *B. hattahensis* Geddes 1981, *B. kadjikadji* Timms 2002, *B. lamellata* Timms and Geddes 2003, *B. longirostris* Wolf 1911, *B. lyrifera* Linder 1941, *B. nana* Timms 2002, *B. nichollsi* Linder 1941, *B. occidentalis* Dakin 1914, *B. pinnata* Geddes 1981, *B. proboscida* Henry 1924, *B. simplex* Linder 1941, *B. wellardi* Milner 1929, *Parartemia contracta* Linder 1941, *P. cylindrifera* Linder 1941, *P. informis* Linder 1941, *P. minuta* Geddes 1973, *P. zietziana* Sayce 1903, *Streptocephalus queenslandicus* Herbert and Timms 2000, *Streptocephalus n. sp.* a, *Streptocephalus n. sp. b* and an undescribed branchiopodid anostracan (all three from the Paroo, nw NSW-sw Qld - Timms and Sanders 2002 and Timms unpublished data. Two different cyst types were found in *Branchinella occidentalis*. Full descriptions could not be made for *Branchinella affinis, B. nana* and *Parartemia informis* due to the presence of only immature cysts. Locality and collection details for each species are listed in Appendix 1. The described Australian fairy shrimp species for which we did not have cysts include the following: *Branchinella apophystata* Linder 1941, *B. compacta* Linder 1941, *B. denticulata* Linder 1941, *B. halsei* Timms 2002, *B. insularis* Timms and Geddes 2003, *B. latzi* Geddes 1981, *B. tyleri* Timms and Geddes 2003, *Parartemia extracta* Linder 1941, *P. longicaudata* Linder 1941, *P. serventyi* Linder 1941 and *Streptocephalus archeri* Sars 1896.

The cyst characteristics of Australian anostracans are as follows.

### Family Parartemidae

*Parartemia contracta* Linder

Cyst shape spherical (Fig. 1). Cyst size 250-275 µm (mean = 263.3; n = 10). External surface with some inpocketing, adjacent inpockets separated by indistinct ridges; individual cysts with 2-6 inpockets; surface smooth. Alveolar layer (Fig. 2) uniform; short struts; vesicles small rounded and subequal. Tertiary layer thin.

*Parartemia cylindrifera* Linder

Cyst shape spherical (Fig. 3). Cyst size 204-225 µm (mean = 214.6; n = 10). External surface with some inpocketing; adjacent inpockets separated by ridges; individual cysts with several inpockets each; surface smooth. Alveolar layer uniform, mostly solid (Fig. 4). Tertiary layer thin.

*Parartemia informis* Linder

Immature cyst shape spherical. Cyst size 162-176 µm (mean = 167.5; n = 10).

*Parartemia minuta* Geddes

Cyst shape spherical (Fig. 5). Cyst size 180-232 µm (mean = 208.0; n = 30). External surface with inpocketing; adjacent inpockets separated by ridges; individual cysts with several inpockets each; surface smooth. Alveolar layer uniform and solid (Fig. 6). Tertiary layer thin.

*Parartemia zietziana* Sayce

Cyst shape spherical to hemispherical (Figs. 7-8). Cyst size 180-208 μm (mean = 192.7; n = 11). External surface with inpocketing; inpocketing usually at one end; adjacent inpockets separated by ridges; ridges usually with sloping walls and rounded tops; surface smooth. Alveolar layer uniform and solid (Fig. 9). Tertiary layer thin.

**Family Branchiopodidae**

undescribed branchiopod genus and species

Cyst shape very irregularly spherical (Fig. 10), with projecting flanges that interlock with those of other cysts binding the cyst mass together (Fig. 11). Cyst diameters 208-250 μm (mean = 229.7; n = 20). External surface with ridges defining irregular polygons; intersecting ridges often extending as flanges; entire surface covered with shallow, rounded to polygonal depressions; polygon size variable and larger on flanges and ridges (Fig. 12). Cortex relatively thick (» 2 μm); one layer of short columns, columns parallel to each other and perpendicular to the surface. Alveolar layer (Fig. 13) thin; with small and uniform vesicles. Tertiary base thin.

**Family Streptocephalidae**

*Streptocephalus queenslandicus* Herbert and Timms

Cyst shape tetrahedral (Fig. 14-15); cyst size 169-208 μm (mean = 195; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges each with 2 longitudinal grooves in middle half producing 3 short ridge crests; intersecting ridges flare outward; triangular faces gently convex with 1 or 2 small bumps midface; surface granular. Alveolar layer (Fig. 16) with 2 sublayers; inner sublayer with short straight struts and medium-sized vesicles and hollows; outer sublayer uniform and solid; vesicular layer extends outward into ridge intersections. Tertiary layer thin.

*Streptocephalus n. sp. a* (locality: Pine Tree Pool, Budgerie Paddock, Bloodwood Station, 130 km NW of Bourke, NSW)

Cyst shape tetrahedral (Fig. 17); cyst size 254-300 μm (mean = 283.0; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges with nearly vertical sides, top rounded (Fig. 18), middle half of ridge along each face with a series of large punctae on each side, intersecting ridges flare outward; triangular faces flat to convex; surface bumpy. Cortex thick (2-3 μm). Alveolar layer (Fig. 19) with 2 sublayers; inner sublayer with thin short struts defining variably-sized, interconnecting vesicles; outer sublayer uniform and solid. Tertiary layer thin.

*Streptocephalus n. sp. b* (locality: Box Hole, on road 3 km south of homestead, Currawinya National Park, SW QLD)

Cyst shape tetrahedral (Fig. 20); cyst size 240-268 μm (mean = 249.3; n = 20). External surface with ridges dividing surface into 4 triangular faces; ridges each with 2 longitudinal grooves in middle producing 3 short ridge crests (Fig. 21); intersecting ridges producing rounded corners; triangular faces depressed, flattened, with small bumps midface; surface mildly bumpy. Alveolar layer (Fig. 22) vesicular; inner vesicles smaller; vesicles under ridges larger. Tertiary layer thin.

**Family Thamnocephalidae**

*Branchinella affinis* Linder

Cyst shape spherical (Fig. 23). Cyst diameter 95-134 μm (mean = 113.2; n = 20). External surface with steep-walled, arcuate ridges defining pinched polygons.

*Branchinella arborea* Geddes

Cyst shape spherical (Fig. 24). Cyst size 183-201 μm (mean = 191.6; n = 10). External surface with ridges defining flat-bottomed polygons; ridges straight-sided, surface covered with small punctae (Fig. 25). Alveolar layer (Fig. 26) with 2 sublayers; inner sublayer with small subequal vesicles; outer sublayer with long struts and large hollows. Tertiary base thin.

*Branchinella australiensis* (Richters)

Cyst shape spherical (Fig. 27). Cyst size 197-222 μm (mean = 213.5; n = 10). External surface with ridges defining polygons; ridges straight-walled, top pinched into a bead running along ridge, bead with pores (Fig. 28); polygons with flat bottoms. Alveolar layer (Fig. 29) with variably-sized vesicles; inner vesicles usually smaller than outer ones. Tertiary base thin.

*Branchinella basipina* Geddes

Cyst shape spherical (Fig. 30). Cyst size 225-275 μm (mean = 253.5; n = 10). External surface with ridges defining pinched polygons; ridges with sloping sides, tops evenly rounded; polygons with concave bottoms; surface rugose. Alveolar layer (Fig. 31) with small, subequal vesicles. Tertiary base thin.

*Branchinella buchananensis* Geddes

Cyst shape spherical (Fig. 32). Cyst size 204-232 μm (mean = 217.9; n = 10). External surface with ridges defining pinched polygons; ridges with sloping sides; polygons with concave bottoms; surface rugose. Alveolar layer (Fig. 33) with 2 sublayers; inner sublayer with small subequal vesicles; outer sublayer with long branching struts and large unequal vesicles. Tertiary base thin.

*Branchinella budjiti* Timms

Cyst shape spherical (Fig. 34). Cyst size 141-155 μm (mean = 144.7; n = 23). External surface with sinuous ridges defining tightly pinched polygons; ridges steep-sided with rounded tops; polygons with sinuous valley-like bottoms; surface slightly bumpy. Alveolar layer (Fig. 35) with 2 sublayers; inner layer with small vesicles; outer sublayer with long parallel struts and large hollows. Tertiary layer thin.

*Branchinella campbelli* Timms

Cyst shape spherical (Fig. 36). Cyst size 162-194 μm (mean = 172.3; n = 20). External surface with broad ridges defining pinched polygons; ridges with sides sloped to vertical, ridge tops very broad; surface scaley. Alveolar layer (Fig. 37) thick, with small to moderate sized vesicles. Tertiary layer thin.

*Branchinella complexidigitata* Timms

Cyst shape spherical (Fig. 38). Cyst size 211-307 μm (mean = 251.0; n = 40). External surface with ridges defining irregular polygons; ridges narrow, steep-sided, midline of ridges with sharp-pointed projections (Figs. 39-40); polygons with bottom flat to concave; surface smooth to scaley and porous. Alveolar layer (Fig. 41) thin; small to medium sized circular vesicles. Tertiary base thin.

*Branchinella dubia* (Schwartz)

Cyst shape spherical (Fig. 42). Cyst size 187-215 μm (mean = 197.1; n = 32). External surface with ridges defining polygons; ridges straight, steep-walled and narrow; polygons with bottoms flat to slightly concave; surface covered with short wrinkles, pores abundant (Fig. 43). Alveolar layer (Fig. 44) with 2 sublayers; inner sublayer with small rounded subequal vesicles; outer sublayer with long sometimes branching struts and large hollows. Tertiary base thin.

*Branchinella frondosa* Henry

Cyst shape spherical (Fig. 45). Cyst size 185-211 μm (mean = 196.1; n = 10). External surface with ridges defining polygons; ridges with sloping sides, tops rounded; polygons with bottom flat to slightly concave; surface smooth. Alveolar layer (Fig. 46) with 3 sublayers; inner sublayer with small vesicles; middle sublayer with long sometimes branching struts and large hollows; outer sublayer with medium-sized vesicles. Tertiary base thin.

*Branchinella hattahensis* Geddes

Cyst shape spherical (Fig. 47). Cyst size 254-289 μm (mean = 268.9; n = 20). External surface with ridges defining polygons; ridges with steep sloping sides, ridge tops with a sinuous bead and sharp-pointed and sometimes recurved projections (projections sometimes with film between) (Figs. 48-49); polygons with bottoms flat to slightly concave; surface strongly rugose or bumpy. Alveolar layer (Fig. 50) with 2 sublayers; inner sublayer with small- to medium-sized rounded vesicles; outer sublayer with narrow curving struts and large hollows. Tertiary base thin.

*Branchinella kadjikadji* Timms

Cyst shape spherical (Fig. 51). Cyst size 254 μm (n = 2). External surface with ridges defining polygons; ridges steep-sided and sinuous, tops with rounded bead; polygons irregularly shaped, bottoms flat; surface smooth (Fig. 52). Alveolar layer (Figs. 53-54) with at least 2 sublayers; outer sublayer with medium-sized rounded vesicles; next sublayer inside with short struts and large hollows. Tertiary base not visible in available cross-sections.

*Branchinella lamellata* Timms & Geddes

Cyst shape spherical (Fig. 55). Cyst size 124-180 μm (mean = 147.6; n = 31). External surface with ridges defining polygons; ridges with sloping sides and rounded tops; polygons irregular and highly pinched, bottoms concave; surface bumpy. Alveolar layer (Fig. 56) with narrow struts and very large hollows. Tertiary base thin.

*Branchinella longirostris* Wolf

Cyst shape spherical (Fig. 57). Cyst size 264-300 -μm (mean = 276.9; n = 29). External surface with ridges defining polygons; ridges very narrow, not always connecting to other ridges, ridge junctions extended into spines with tips that are bifid, trifid or recurved (Fig. 58); polygons with concave bottoms; surface bumpy to scaley. Alveolar layer (Fig. 59) mostly hollow with very narrow struts. Tertiary base thin.

*Branchinella lyrifera* Linder

Cyst shape spherical; inpocketing common (Figs. 60). Cyst size 158-183 μm (x = 171.5; n = 20). External surface with numerous short flat-topped columns, columns often connected by ridges; ridges of variable widths (Figs. 61-62). Alveolar layer solid (Fig. 63). Tertiary base thin.

*Branchinella nana* Timms

Immature cyst shape spherical. Cyst size 144-158 μm (mean = 152.3; n = 19).

*Branchinella nichollsi* Linder

Cyst shape spherical (Fig. 64). Cyst size 187-247 µm (mean = 202.3; n = 30). External surface with ridges defining polygons; ridges narrow, steep-sided, with zig-zag patterns, tops with narrow bead (Fig. 65); polygons tightly pinched, bottoms flat to concave; surface slightly bumpy. Alveolar layer (Fig. 66) mostly hollow, with very thin struts. Tertiary base thin.

*Branchinella occidentalis* Dakin (two cyst morphs)

Type I cyst: Cyst shape spherical; inpocketing common (Fig. 67). Cyst size 257-328 µm (mean = 283.5; n = 20). External surface with narrow sinuous ridges defining small, irregular, pinched polygons; ridges steep-sided and short. Alveolar layer (Fig. 68) not well developed. Tertiary base not seen.

Type II cyst: Cyst shape spherical (Fig. 69). Cyst size 550-571 µm (mean = 565.3; n = 20). External surface with ridges defining rounded depressions; ridges narrow except where intersecting, sides vertical, tops flat; rounded depressions with bottoms slightly concave and extremely porous (Fig. 70); surface smooth. Alveolar layer (Fig. 71) with 3 sublayers; inner sublayer with small equal rounded vesicles; middle sublayer with few struts, mostly open hollows, pores connecting to outside; outer layer with stringy vermiform struts, connecting to inner side of external surface. Tertiary layer thin.

*Branchinella pinnata* Geddes

Cyst shape spherical (Fig. 72). Cyst size 173-190 µm (mean = 181.1; n = 10). External surface with ridges defining pinched polygons; ridges with sides nearly vertical, tops rounded; polygons irregular in shape, bottoms flat to concave; surface very bumpy. Alveolar layer (Fig. 73) with 3 sublayers; inner sublayer with small rounded subequal vesicles; middle layer with long branching struts and large hollows; outer sublayer with medium-sized irregularly shaped vessicles. Tertiary layer thin.

*Branchinella probiscida* Henry

Cyst shape spherical (Fig. 74). Cyst size 158-187 µm (mean = 174.9; n = 19). External surface with ridges defining polygons; ridges vermiform with sides nearly vertical, tops smooth and rounded; polygons irregular in shape, some pinched, bottoms slightly concave and with pores; surface generally smooth (Fig. 75). Alveolar layer (Fig. 76) without distinct sublayers; struts usually short; vesicles irregular in shape and variable in size. Tertiary layer thin.

*Branchinella simplex* Linder

Cyst shape spherical (Fig. 77). Cyst size 144-201 µm (mean = 176.4; n = 32). External surface with ridges defining polygons; ridges with sides slightly sloping to vertical; polygons pinched, bottoms concave; surface smooth with irregularly spaced punctae. Alveolar layer (Fig. 78) uniform; short branching struts and medium-sized hollows. Tertiary layer thin.

*Branchinella wellardi* Milner

Cyst shape spherical (Fig. 79). Cyst size 158-176 µm (mean = 168.4; n = 30). External surface with ridges defining polygons; ridges narrow and steep-sided, tops sharp except broader at intersections (Fig. 80); polygons irregular in shape, some pinched, bottoms concave to flat; surface punctate to porous. Alveolar layer (Fig. 81) uniform, thick; short struts with small interconnected vesicles. Tertiary layer thin.

## DISCUSSION

Australia is currently experiencing a surge of interest in its fairy shrimps, as indicated by the large percentage of newly described species and species awaiting description (Timms, in press). Species descriptions omit information on cyst shells, but suitable descriptions for many species are provided here. Although about 40% of known species are yet to be studied (and for most of these, data are unlikely to be available in the near future), enough descriptions of cyst shell morphology are available for comparison between Australian and overseas fauna and among the Australian species.

Cysts of the species examined could be easily separated at the genus level, but only with difficulty or not at all at the species level. The most distinctive are those of *Streptocephalus* with their overall tetrahedral shape and distinct facet-edge ridges and convex to concave faces with bumps. This feature places them within the *sudanicus* species group of Maeda-Martínez et al. (1995) and subgenus *Parastreptocephalus* of Brendonck et al. (1992); *Streptocephalus* species with mature spherical cysts have yet to be found in Australia.

Cysts of the new branchiopodid genus are also distinctive because of flanges from ridges defining irregular polygons. Almost all of the species of *Branchinella* have cysts with a polygonal surface largely reminiscent of those of overseas members of the genus (Belk and Sisson 1992, Mura 1992, Brendonck and Riddoch 1997; Sanoamuang et al. 2003). Cysts of *B. lyrifera* are discordant for the genus because they are covered with flat-topped columns with little evidence of polygons, though the columns are connected by uncoordinated ridges.

Cysts of *Parartemia*, an Australian endemic genus, are described for the first time. They are smooth, rather like those of *Artemia* (Hill and Shepard 1997), but with some inpocketing. Given possible undetected variation within species, particularly in those subjected to predation (Mura et al. 2002), it is unwise to compare species within genera.

None of the Australian cysts examined here have extreme anti-predation devices such as honeycombing or long spines (Dumont et al. 2003). Some species have minor protruding structures which may assist against predation. The most developed are the bifid/trifid/recurved spines at ridge junctions in *B. longirostris*. Interestingly this species lives in gnammas (rock pools) in which many potential predators live including flatworms (Pinder et al. 2000). Other species of *Branchinella* with small spines include *B. complexidigitata* in which they are sharp pointed and *B. hattahensis* where the spines are recurved. The flanges on the cysts of the undescribed branchipodid genus could be antipredation devices, but another explanation is that they assist in holding the egg mass together (as observed when trying to separate the cysts). The value of such a strategy is questionable, given the decreased possibly of dispersal of a clumped egg mass, but perhaps it helps to deter egg predators.

The cyst shell structure (especially the cross-sectional structure) in this study ranged from relatively simple (e. g., in *Parartemia*) to complex (e. g., in *Branchinella budjiti* and an undescribed branchipodid genus). During the examination of *Branchinella occidentalis* the first set of cysts appeared to be not completely mature so a second set was examined. This second set was of a very different size and form. Thus, it appears that either the species has two different cyst morphs or there may be a cryptic species in what is now known as *B. occidentalis*. At least other species are known to have two cyst types: *Eubranchipus serratus* (Hill and Shepard 1997) and *Streptocephalus sealii* (R. Hill, pers.com.). During the course of this study the only cyst structure found that has not been seen in any other fairy shrimp before was the external flanges and the parallel columns in the cortex of the undescribed genus of branchipodid fairy shrimp. Therefore, with minor exception, the maximum range of structural diversity in cysts may have been described. Whether or not this is true will be decided by examination of the remaining undescribed cysts of other world genera.

The structure of the cyst shell, especially in the alveolar layer, begs a functional explanation. It is likely that the structure represents a compromise between crush-resistance and rehydration ability. But other functions that have been suggested include: protection from abrasion and ultraviolet light (Belk 1969); a float for cysts (Morris and Afzelius 1967); a barrier against physio-chemical stresses and an aid to gaseous exchange (Tommasini and Sabelli 1989); an anti-predation device (Dumont et al. 2003) and, dispersal aids or inhibitors (Brendonck et al. 1992).

## ACKNOWLEDGEMENTS

We thank Bruce Scott for his masterful supervision of the scanning electron microscope.

## REFERENCES

Belk, D.. (1969). Functions of the conchonstracan eggshell. *Crustaceana* **19(1)**, 106-107.

Belk, D. and Sissom, S. (1992). New *Branchinella* (Anostraca) from Texas, U.S.A., and the problem of antennalike processes. *Journal of Crustacean Biology* **12**, 312-316.

Brendonck, L. and Coomans, A. (1994a). Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 1: South of Zambezi and Kunene rivers. *Archiv Hydrobiologia/Supplement* **99** **(3)**, 313-334.

Brendonck, L. and Coomans, A. (1994b). Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 2: North of Zambezi and Kunene rivers, and Madagascar. *Archiv Hydrobiologia/Supplement* **99** **(3)**, 335-356.

Brendonck, L. and Riddcoh, B. (1997). Anostracans (Branchiopoda) of Botswana: Morphology, Distribution, Diversity, and Endemicity. *Journal of Crustacean Biology* **17**, 111-134.

Brendonck, L., Hamer, M. and Thiéry, A. (1992). Occurrence of tetrahedral eggs in the Streptocephalidae Daday (Branchiopoda: Anostraca) with descriptions of a new subgenus, *Parastreptocephalus*, and a new species, *Streptocephalus (Parastreptocephalus) zuluensis* Brendonck and Hamer. *Journal Crustacean Biology* **12**, 282-297.

Brendonck. L., Thiéry, A. and Coomans, A. (1990). Taxonomy and biogeography of the Galapagos branchiopod fauna (Anostraca, Notostraca, Spinicaudata). *Journal Crustacean Biology* **10**, 676-694.

Dakin, W.J. (1914). Fauna of Western Australia. II The Phylllopoda of Western Australia. *Proceedings Zoological Society London* **1914**, 293-305.

DeWalsche, C. Munuswamy, N. and Dumont, H. J. (1991). Structural differences between the cyst walls of *Streptocephalus dichotomus* (Baird), *S. torvicornis* (Waga), and *Thamnocephalus platyurus* (Packard) (Crustacea: Anostraca), and a comparison with other genera and species. *Hydrobiologia* **212**, 195-202.

Dumont, H.J., Nandini, S. and Sarma, S.S.S. (2003). Cyst ornamentation in aquatic invertebrates: a defence against egg-predation. *Hydrobiologia* **486**, 161-167.

Geddes, M.C. (1973). Studies on Australian Anostracans (Crustacea: Branchiopoda). Ph. D. thesis. Monash University. 282 pp.

Geddes, M.C. (1981). Revision of Australian species of *Branchinella* (Crustacea: Anostraca). *Australian Journal of Marine and Freshwater Research* **32**, 253-295.

Hamer, M., Brendonck, L. Coomans, A. and Appleton, C. C. (1994). A review of African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 1: South of Zambezi and Kunene rivers. *Archiv Hydrobiologia/Supplement* **99 (3)**, 235-277.

Hamer, M., Brendonck, L. Coomans, A. and Appleton, C. C. (1994). A review of African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 2: North of Zambezi and Kunene rivers and Madagascar. *Archiv Hydrobiologia/Supplement* **99 (3)**, 279-311.

Henry, M. (1924). A monograph on the freshwater Entomostraca of New South Wales. IV Phyllopoda. *Proceedings Linnean Society New South Wales* **49**, 120-137.

Herbert, B. and Timms, B.V. (2000). A new species of *Streptocephalus* (*Parastreptocephalus*) (Crustacea: Anostraca: Streptocephalidae) from North Queensland, Australia. *Memoirs of the Queensland Museum* **45**(2), 385-390.

Hill, R.E. and Shepard, W.D. (1997). Observations on the identifications of California anostracan cysts. *Hydrobiologia* **359**, 113-123.

Linder, F. (1941). Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. *Zoologiska Bidrag från Uppsala* **20**, 101-302.

Maeda-Martínez, A.M., Belk, D., Obregón-Barboza, H and Dumont, H.J. (1995). A contribution to the systematics of the Streptocephalidae (Branchiopodidae: Anostraca). *Hydrobiologia* **298**, 203-232.

McMaster, K., Savage, A., Finston, T. Johnson, M.S. and Knott, B. (In Press). Has *Artemia parthenogenetica* been introduced into Western Australia through human agency? *Hydrobiologia*

Milner, D.F. (1929). A description of two new species of Anostraca Phyllopoda from Western Australia. *Journal Royal Society of Western Australia* **15**, 25-35.

Morris, J. E. and Afzelius, B. A. (1967). The structure of the shell and outer membranes in encysted *Artemia salina* embryos during cryptobiosis and development. *Journal Ultrastructure Research* **20**, 244-259.

Mura, G. (1986). SEM morphological survey on the egg shell of Italian anostracans (Crustacea, Branchiopoda). *Hydrobiologia* **134**, 273-286.

Mura, G. (1991a). SEM morphology of resting eggs in the species of the genus *Branchinecta* from North America. *Journal Crustacean Biology* **11**, 432-436.

Mura, G. (1991b). Additional remarks on cyst morphometrics in anostracans and its significance. Part 1: egg size. *Crustaceana* **61**, 241-252.

Mura, G. (1992). Pattern of egg shell morphology in thamnocephalids and streptocephalids of the New World (Anostraca). *Crustaceana* **62**, 300-311.

Mura, G. (2001). Morphological diversity of the resting eggs in the anostracan genus *Chirocephalus* (Crustacea, Branchiopoda). *Hydrobiologia* **450**, 173-185.

Mura, G., Zarattini, P. and Petkowski, S. (2002). Morphological divergences and similarities among *Chirocephalus diaphanous carinatus* populations (Crustacea, Anostraca) from the Balkan area. *Journal of Crustacean Biology* **22**, 162-172.

Pinder, A.M., Halse, S.A., Shiel, R.J. and McRae, J.M. (2000). Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *Journal of the Royal Society of Western Australia* **83**, 149-161.

Richters, F. (1876). *Branchipus australiensis* n. sp. *Journal Museum Godeffroy* **12**, 43-44.

Sanoamuang, L., Saenghan, N., and Murugan, G. (2003). First record of the family Thamnocephalidae (Crustacea: Anostraca) from Southeast Asia and description of a new species of *Branchinella. Hydrobiologia* **486**, 63-69.

Sars, G.O. (1896). Description of two new Phyllopoda from north Australia. *Archiv Mathematik Naturvidensk Christiana* **28**, 4-6.

Sayce, O.A. (1903). The Phyllopoda of Australia, including descriptions of some new genera and species. *Proceedings Royal Society Victoria* **15**, 224-261.

Schwartz, K.Y. (1917). Results of Dr. E Mjobergs Swedish scientific expedition to Australia 1910-1913. XV. Descriptions of two Australian phyllopods. *K. Sven. Vetenkapsakad. Handl.* **52**, 7-8.

Shepard, W.D. (1999). First record of fairy shrimp in Belize, and a comparison of cyst-shell morphology in the New World members of the *Streptocephalus sealii* species group (Anostraca: Streptocephalidae). *Journal of Crustacean Biology* **19**, 355-360.

Shepard, W.D. and Hill, R.E. (2001). Anostracan cysts found in California salt lakes. *Hydrobiologia* **466**, 149-158.

Thiéry, A. and Champeau, A. (1988). *Linderiella massaliensis*, new species (Anostraca: Linderiellidae), a fairy shrimp from south-eastern France, its ecology and distribution. *Journal Crustacean Biology* **8**, 70-78.

Thiéry, A. and Gasc, C. (1991). Resting eggs of Anostraca, Notostraca and Spinicaudata (Crustacea, Branchiopoda) occurring in France: identification and taxonomical value. *Hydrobiologia* **212**, 245-259.

Timms, B.V. (2001). Two new species of fairy shrimp (Crustacea: Anostraca: Thamnocephalidae: *Branchinella*) from the Paroo, inland Australia. *Records Australian Museum* **53**, 247-254.

Timms, B.V. (2002). The fairy shrimp genus *Branchinella* (Crustacea: Anostraca: Thamnocephalidae) in Western Australia, including a description of four new species. *Hydrobiologia* **486**, 71-89.

Timms, B.V. (In press). A key to the fairy shrimps (Crustacea: Anostraca) of Australia. Cooperative Research Centre Freshwater Ecology Guide, Albury.

Timms, B.V. and Geddes, M.C. (2003). The fairy shrimp genus *Branchinella* Sayce, 1903 (Crustacea: Anostraca: Thamnocephalidae) in South Australia and the Northern Territory, including descriptions of three new species. *Transactions Royal Society of South Australia* **127**, 53-68.

Timms, B.V. and Sanders, P. (2002). Biogeography and ecology of Anostraca (Crustacea) in middle Paroo catchment of the Australian arid-zone. *Hydrobiologia* **486**, 225-238.

Tommasini, S. and Sabelli, F. S. (1989). Eggshell origin and structure in two species of Conchostraca (Crustacea, Phyllopoda). *Zoomorphology* **109**, 33-37.

Wolf, E. (1911). Phyllopoda. In *Die fauna Südwest-Australiense ergebnisse der Hamburgen südwest australischen Forschungsreise 1905* (Eds W. Michaelsen and R. Hartmeyer) (G. Fisher, Jena) Vol 3, pp 251-276.

## APPENDIX 1

Locality data for species examined.

*Branchinella affinis*: Far North Bulla claypan, Rockwell Station, 180 km SW of Cunnamulla, Queensland. 28° 52' S, 144° 56'E, 27-iii-2000.

*Branchinella arborea*: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 1-vi-1999.

*Branchinella australiensis*: Lower Crescent Pool, Bloodwood Station, 130 km NW of Bourke, NSW, 29° 33'S, 144° 52'E, 1-vi-1999.

*Branchinella basispina*: Homestead Dam, Balladonia Station, 220 km E of Norseman, WA. 32° 28'S, 123° 52'E, 3-iii-1975.

*Branchinella buchananensis*: Gidgee Lake, Bloodwood Station, 130 km NE of Bourke, NSW, 29° 33'S, 144° 50'E, 28-ix-1998.

*Branchinella budjiti*: a claypan on Muella Station, 128 km NE of Bourke, NSW, 29° 31'S, 144° 56'E, 6-xii-1999.

*Branchinella campbelli*: Muella Lake, Tredega Station, 140 km NW of Bourke, NSW, 29° 31'S, 144° 53'E, 27-vi-1998.

*Branchinella complexidigitata*: Lake Arro near Eneabba, 300 km N of Perth, WA, 29° 44'S, 115° 10'E, 2-ix-1999.

*Branchinella dubia*: pool 89 km from Derby on the Gibb R Road, Kimberley, WA, 17° 26'S, 124° 36'E, 31-i-1985.

*Branchinella frondosa*: Steves Pool, Muella Station, 128 km NW of Bourke, NSW, 29° 33'S, 144° 55'E, 24-xi-1998.

*Branchinella hattahensis*: Mid Kaponyee Lake, Currawinya National Park, SW Queensland, 28° 50'S, 144° 19'E, 5-vii-1997.

*Branchinella kadjikadji*: claypan on Kadji Kadji Station, 35 km ENE of Morewa, WA, 29° 08'S, 116° 24'E, 14-viii-1998.

*Branchinella lamellata*: a claypan near Warburton Crossing, Clifton Hills Station, NE South Australia, 27° 02'S, 138° 53'E, 5-xii-2000.

*Branchinella longirostris*: Warrdagga Rock, via Paynes Find, WA, 29° 24'S, 117° 30'E, 26-viii-2001.

*Branchinella lyrifera*: Turkey claypan, Bloodwood Station, 130 km NE of Bourke, NSW, 29° 34'S, 144° 50'E, 1-iv-1999.

*Branchinella nana*: Lake Arrow, near Kalgoorlie, WA, 30° 32'S, 121° 24'E, 14-v-1995.

*Branchinella nichollsi*: Lake Hannan near Kalgoorlie, WA, 30° 40'S, 121° 28'E, 17-iii-1937.

*Branchinella occidentalis*: Freshwater Lake, Bloodwood Station, 130 km NW of Bourke, 29° 29'S, 144° 50'E, 2-vii-1997 (Type I); Plover claypan, Bloodwood Station, 130 km NW of Bourke, 29° 29'S, 144° 48'E, 29-vi-1998 (Type II).

*Branchinella pinnata*: a blackbox swamp, Tredega Station, 140 km NW of Bourke, NSW, 29° 29'S, 144° 52'E, 30-vi-1999.

*Branchinella probiscida*: Darko claypan, Currawinya National Park, SW Queensland, 28° 52'S, 144° 18'E, 4-xii-1999.

*Branchinella simplex*: Lake Arrow, near Kalgoorlie, WA, 30° 32'S, 121° 24'E, 14-v-1995.

*Branchinella wellardi*: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 1-vi-1999

*Parartemia contracta*: small lake adjacent to Lake O'Grady, WA, 30° 25'S, 117° 25'E, ?-viii-1978.

*Parartemia cylindrifera*: Lake Grace, WA, 33° 06'S, 18° 24'E, 24-viii-1978.

*Parartemia informis*: Lake Ballard, WA, 29° 37'S, 121° 07'E, 18-viii-1978.

*Parartemia minuta*: Lower Bell Lake, Bloodwood Station, 130 km NW of Bourke, NSW, 29° 00'S, 144° 48'E, 28-ix-1998.

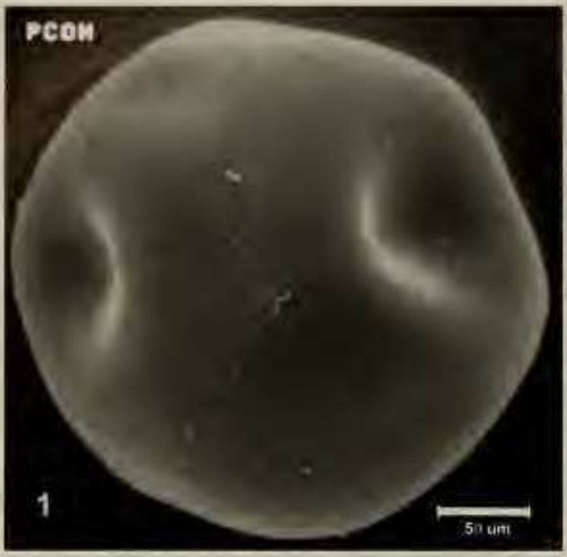
*Parartemia zietziana*: small lake on 'Flowerfield' via Beeac, Victoria, 38° 10'S, 143° 09'E, 15-viii-1970.

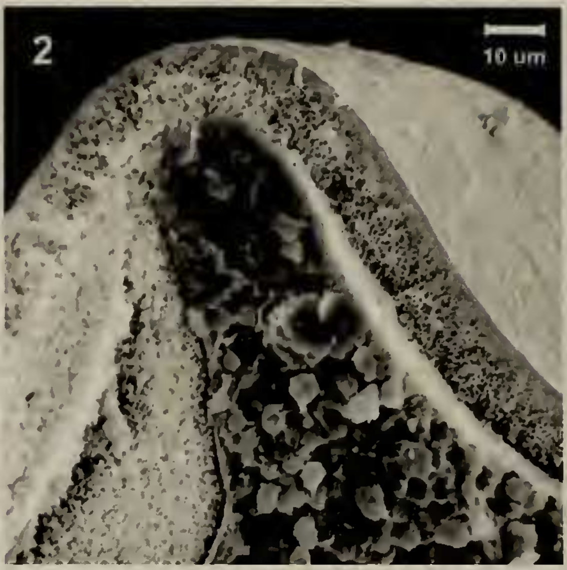
*Streptocephalus queenslandicus*: fish rearing ponds, Walkamin Research Station, via Atherton, Queensland, 17° 08'S, 145° 26'E, ii-1997.

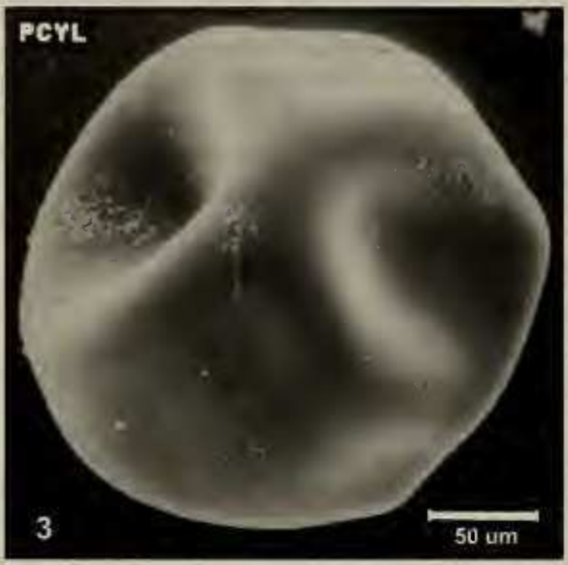
*Streptocephalus* n.sp. a: Pine Tree Pool, Bloodwood Station, 130 km NE of Bourke, NSW, 29 29'S, 144 49'E, 2-xii-1999.

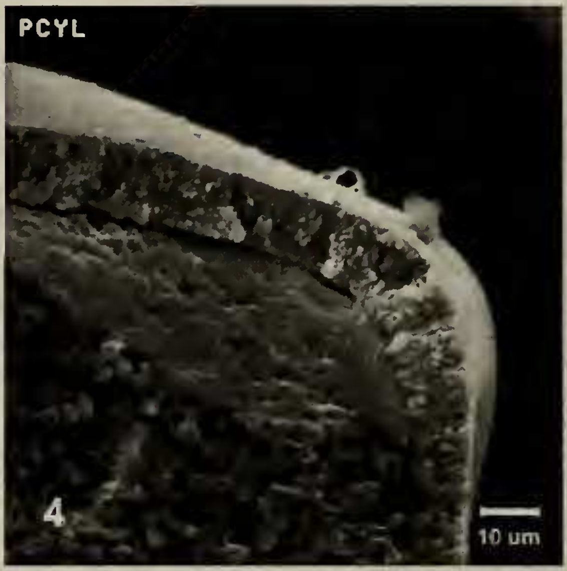
*Streptocephalus* n.sp.b: Box Hole, 4 km S of Homestead, Currawinya National Park, Qld., 28 51'S, 144 29'E, 1-iv-1999.

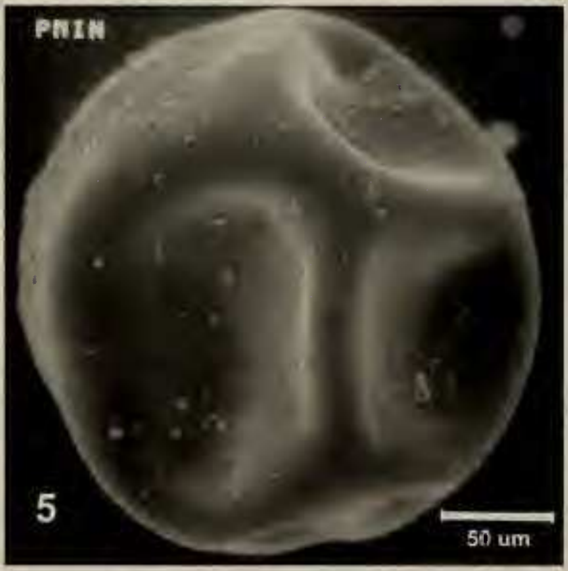
Undescribed new branchiopod genus: Marsilea Pool, Bloodwood Station, 130km NW of Bourke, NSW. 29° 33'S, 144° 52'E, 24-viii-1998.











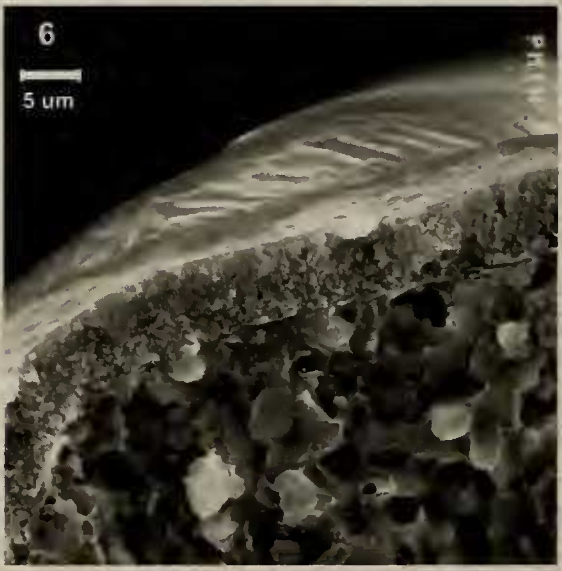
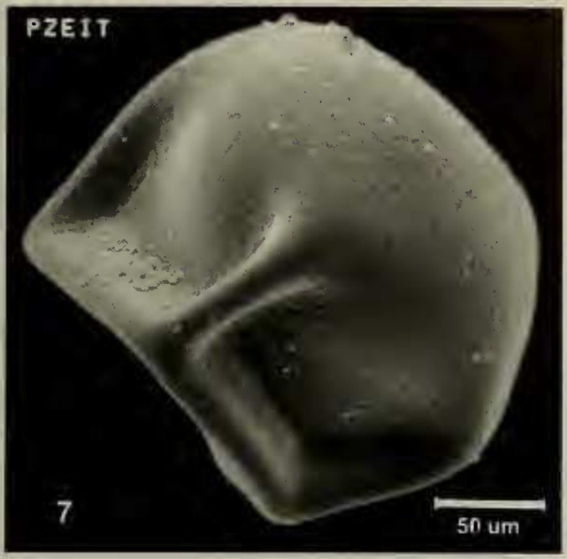
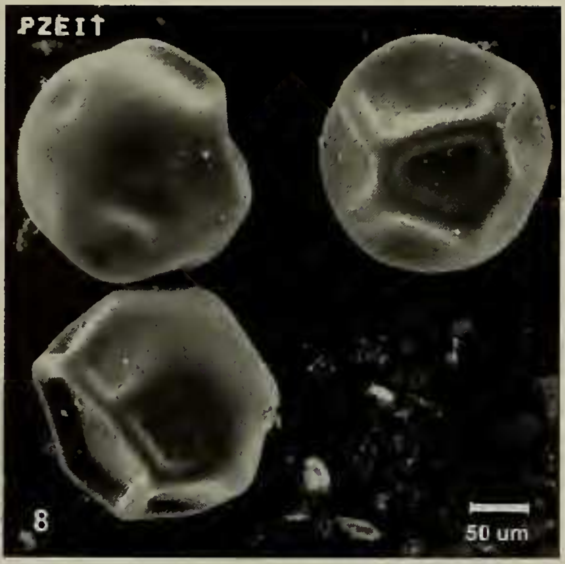
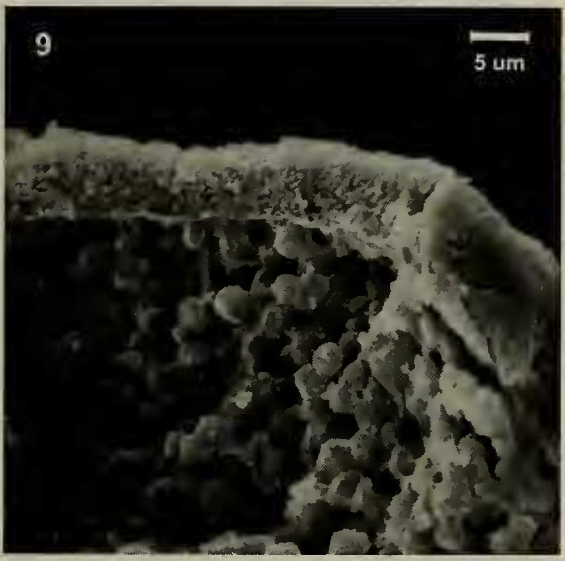
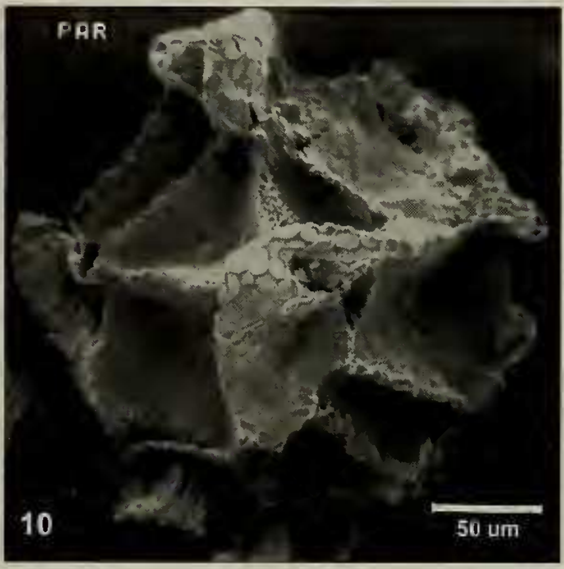


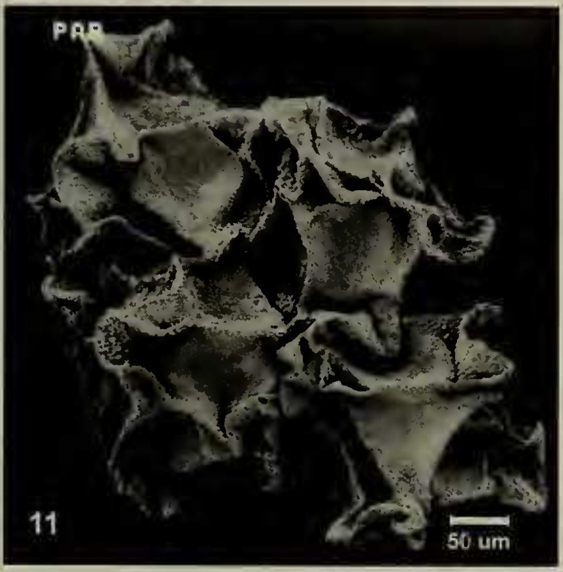
Figure 1. *Parartemia contracta* cyst. Bar = 50 µm.
Figure 2. *Parartemia contracta* cyst shell cross section. Bar = 10 µm.
Figure 3. *Parartemia cylindrifera* cyst. Bar = 50 µm.
Figure 4. *Parartemia cylindrifera* cyst shell cross section. Bar = 10µm.
Figure 5. *Parartemia minuta* cyst. Bar = 50 µm.
Figure 6. *Parartemia minuta* cyst shell cross section. Bar = 5 µm.











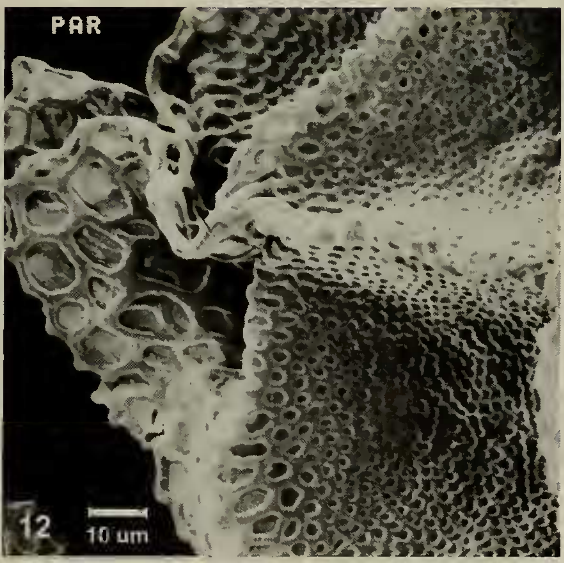
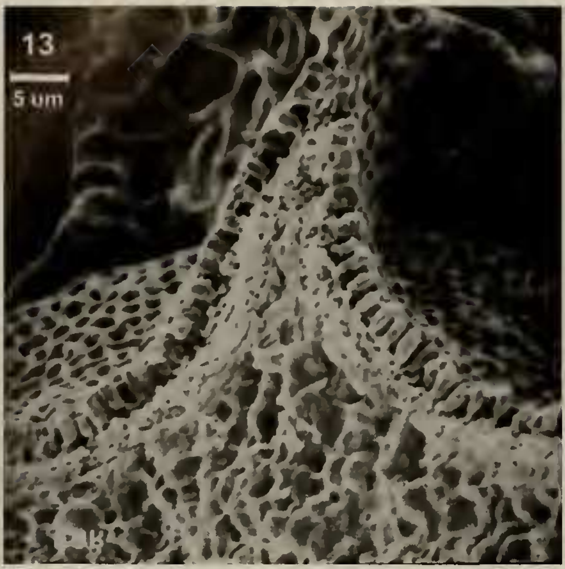
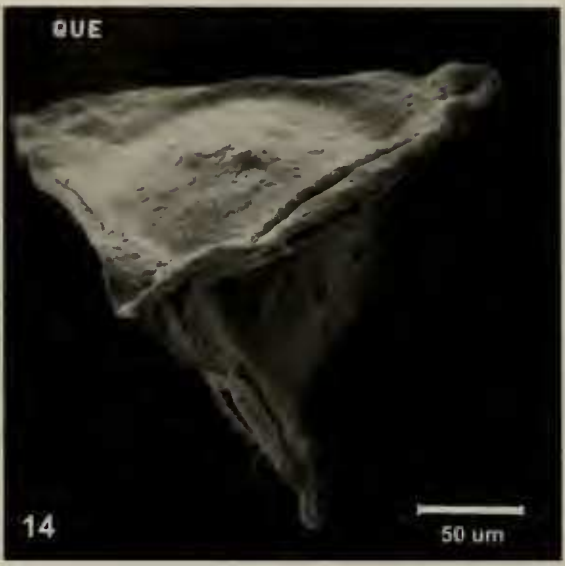
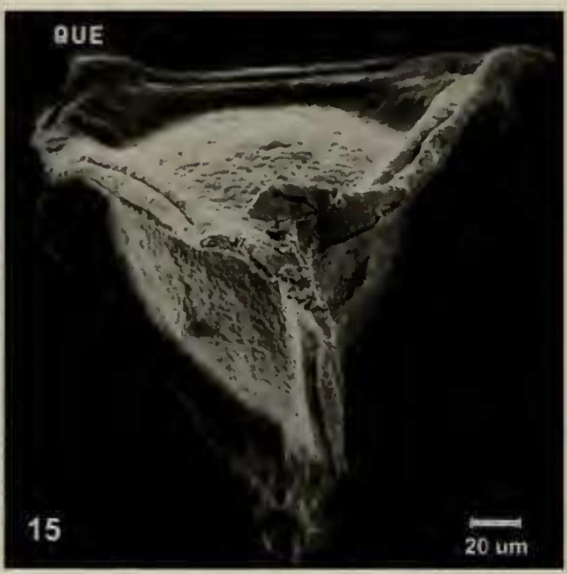
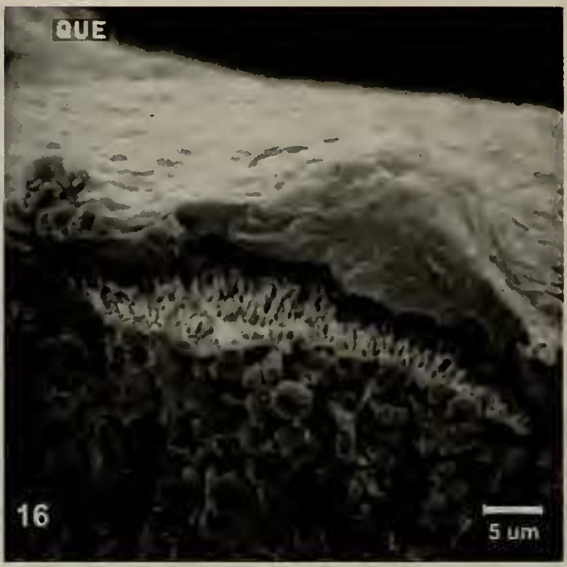


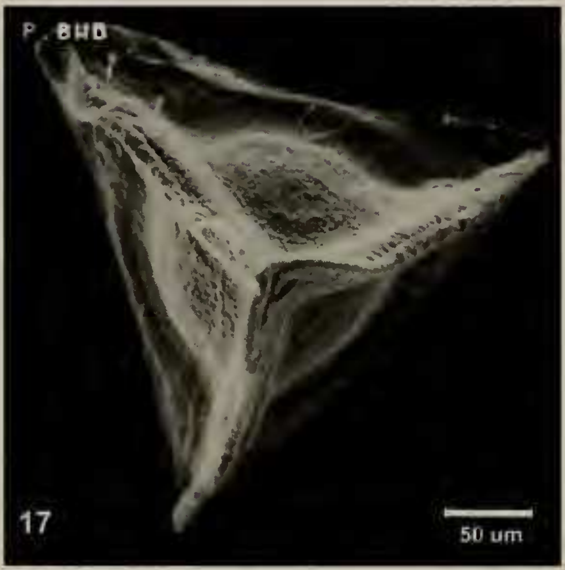
Figure 7. *Parartemia zietziana* cyst. Bar = 50 µm.
Figure 8. *Parartemia zietziana* cyst. Bar = 50 µm.
Figure 9. *Parartemia zietziana* cyst shell cross section. Bar = 5 µm.
Figure 10. Undescribed branchipodid species cyst. Bar = 50 µm.
Figure 11. Undescribed branchipodid species cysts clumped together. Bar = 50 µm.
Figure 12. Undescribed branchipodid species cyst surface. Bar = 10 µm.











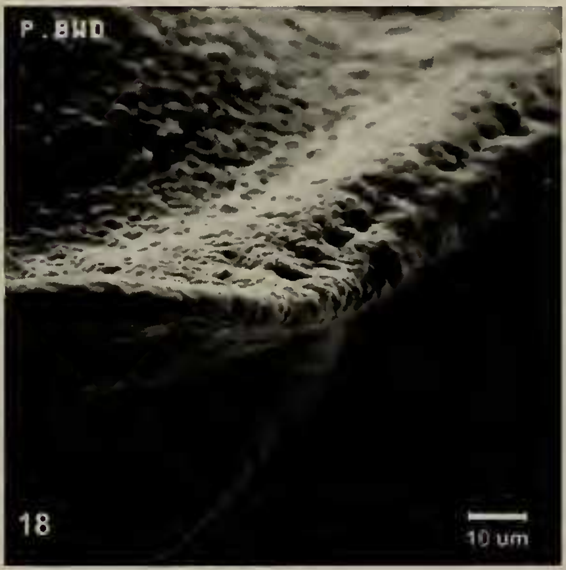
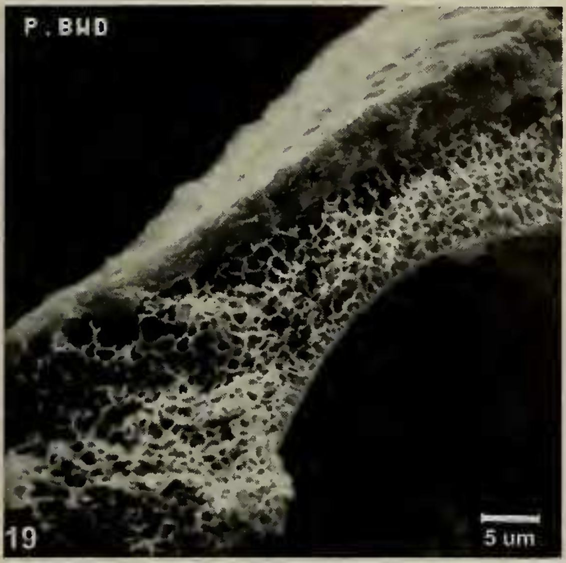
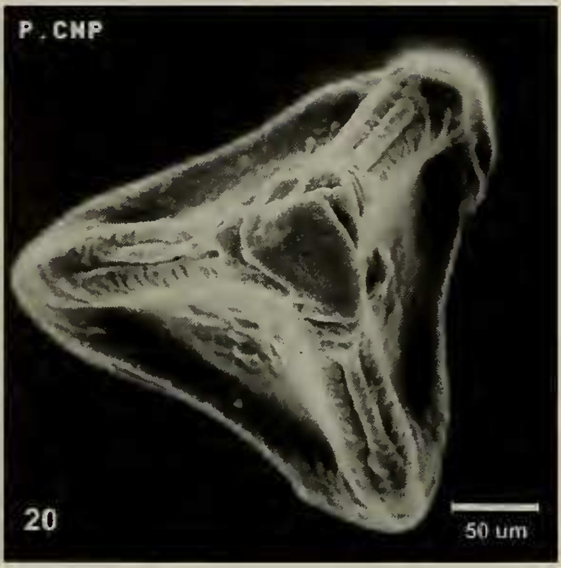
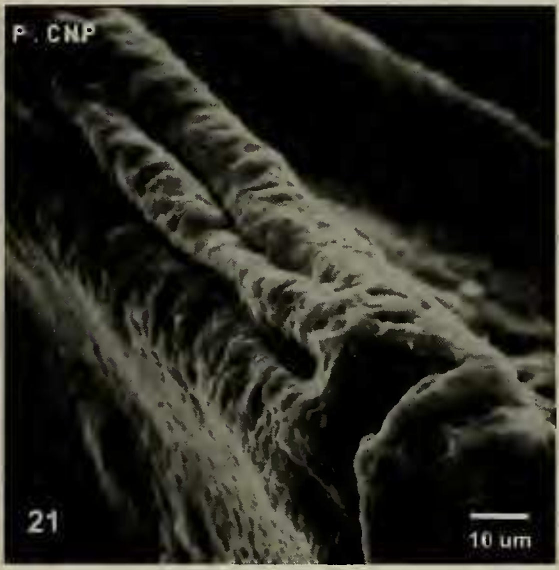
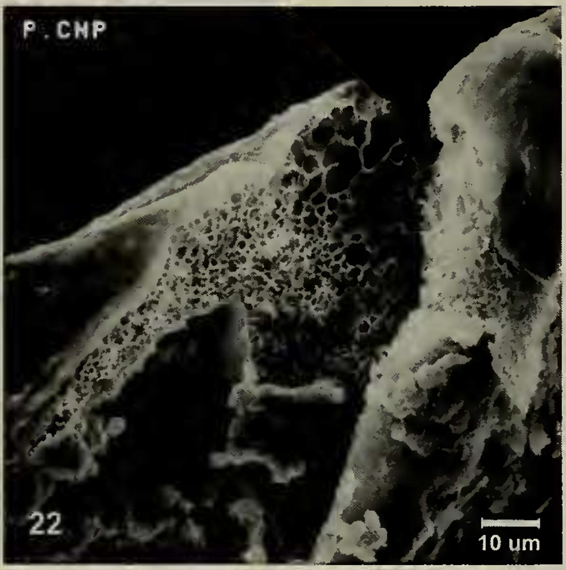


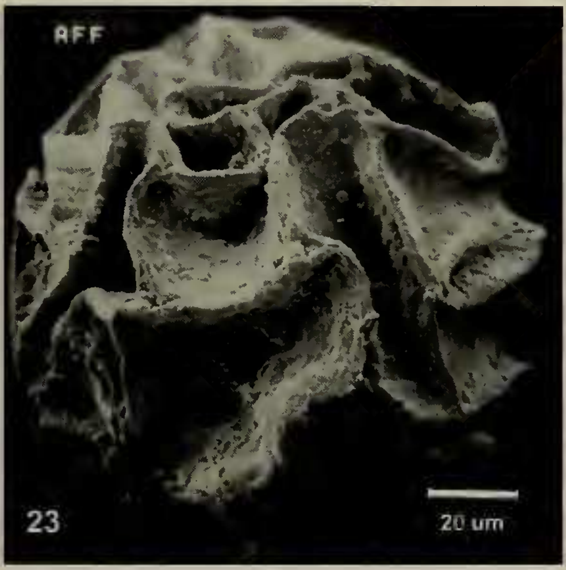
Figure 13. Undescribed branchipodid species cyst shell cross section. Bar = 5 µm.
Figure 14. *Streptocephalus queenslandicus* cyst. Bar = 50 µm.
Figure 15. *Streptocephalus queenslandicus* cyst. Bar = 20 µm.
Figure 16. *Streptocephalus queenslandicus* cyst shell cross section. Bar = 5 µm.
Figure 17. *Streptocephalus* n. sp. a cyst. Bar = 50 µm.
Figure 18. *Streptocephalus* n. sp. a cyst ridges. Bar = 10 µm.











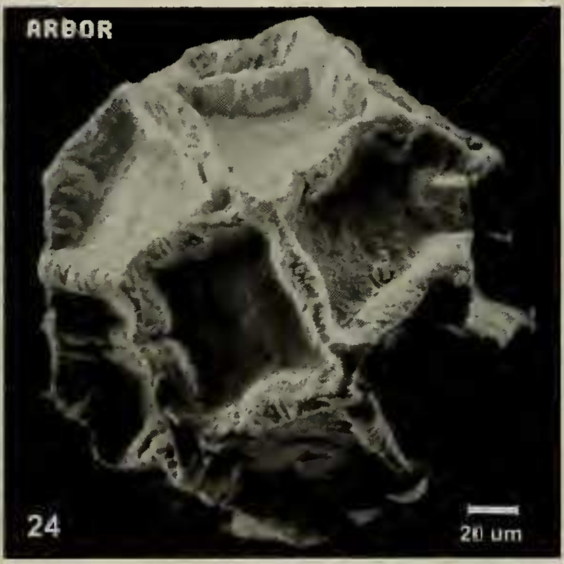
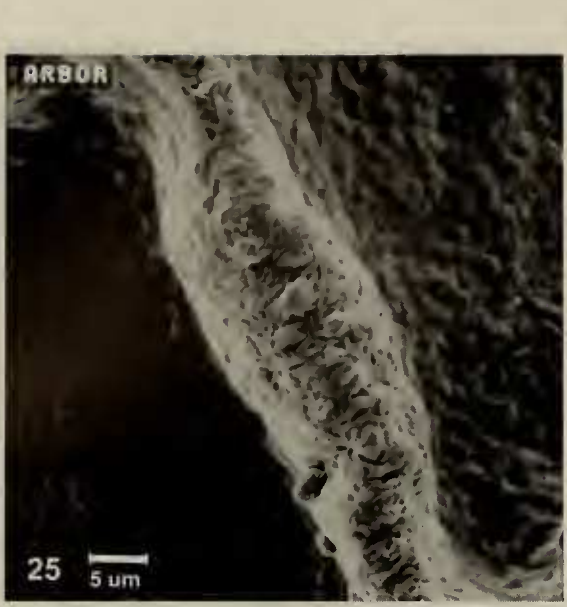
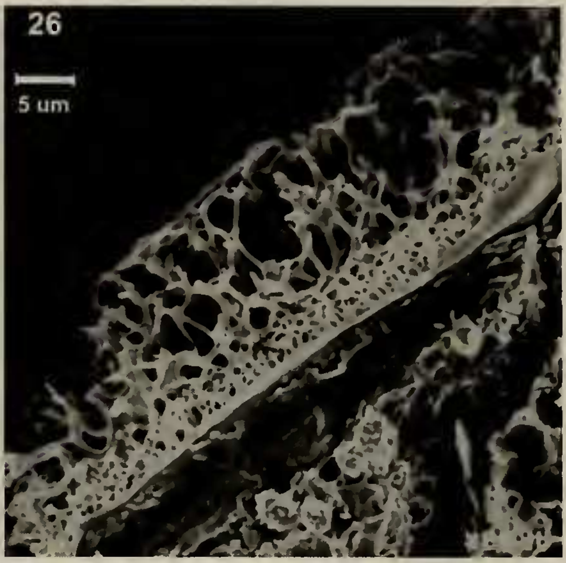
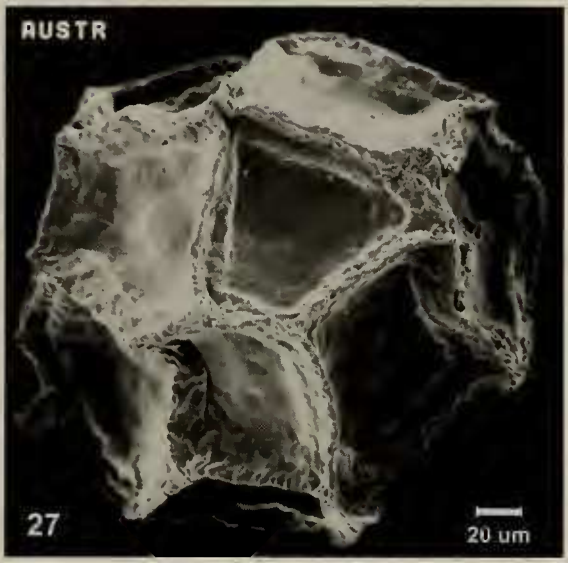
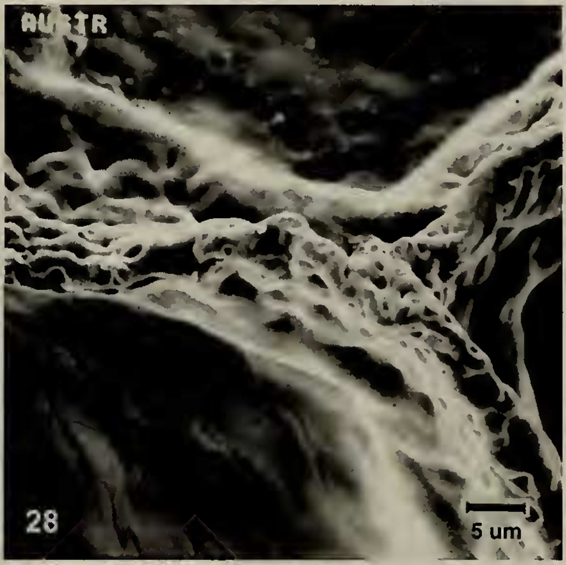


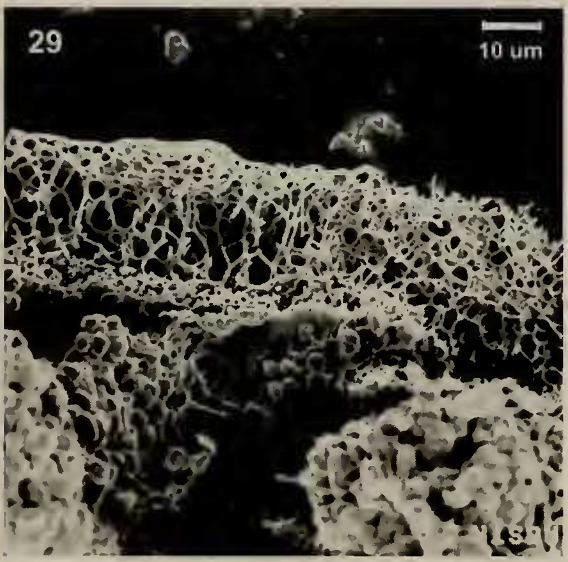
Figure 19. *Streptocephalus* n. sp. a cyst shell cross section. Bar = 5 µm.
Figure 20. *Streptocephalus* n. sp. b cyst. Bar = 50 µm.
Figure 21. *Streptocephalus* n. sp. b cyst ridges. Bar = 10 µm.
Figure 22. *Streptocephalus* n. sp. b cyst shell cross section. Bar = 10 µm.
Figure 23. *Branchinella affinis* cyst (not quite mature). Bar = 20 µm.
Figure 24. *Branchinella arborea* cyst. Bar = 20 µm.











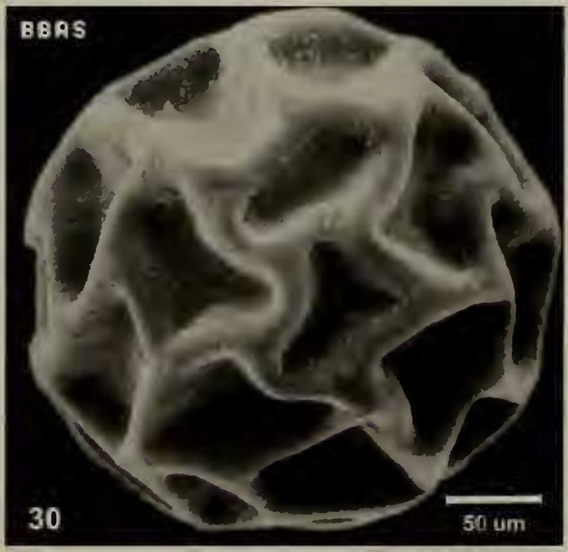
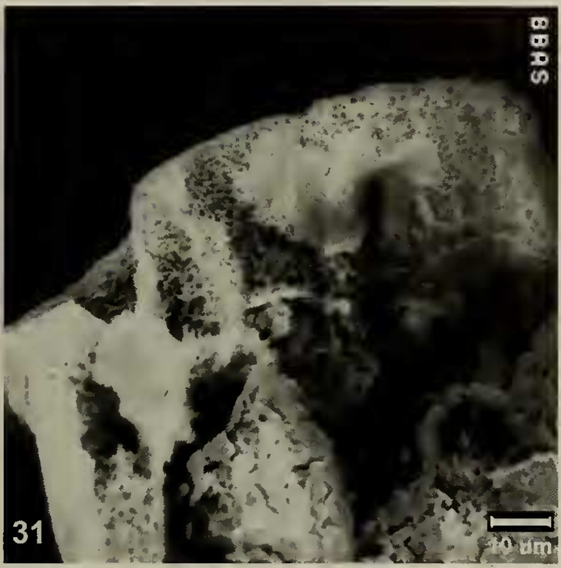
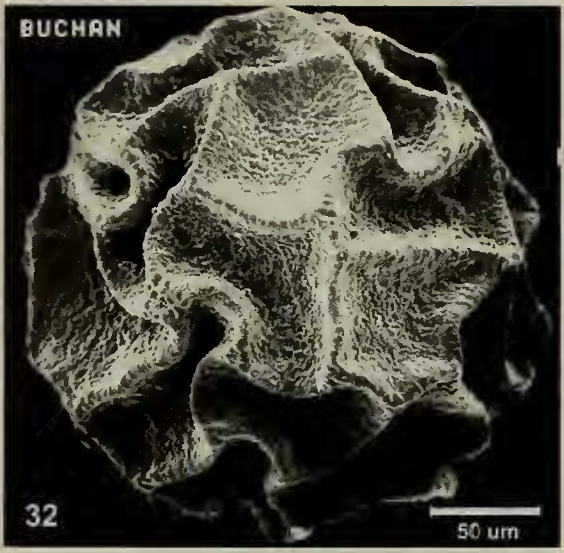
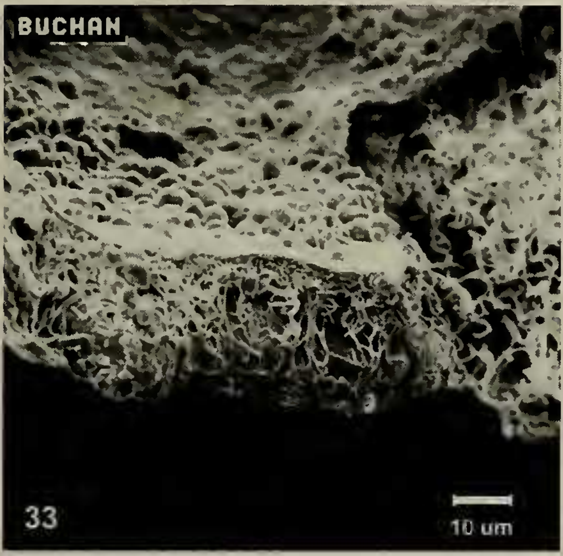
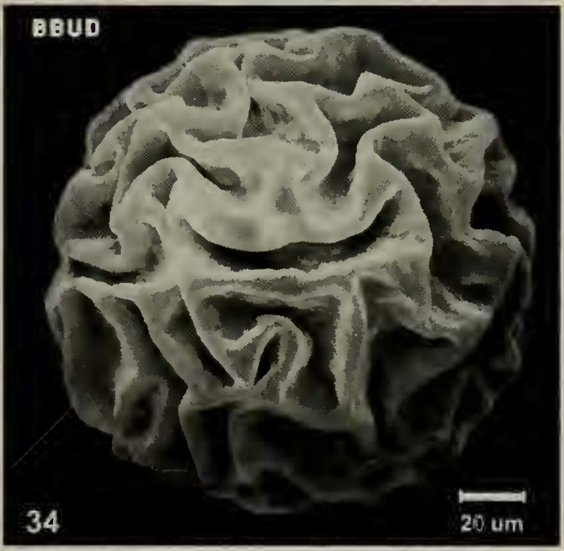


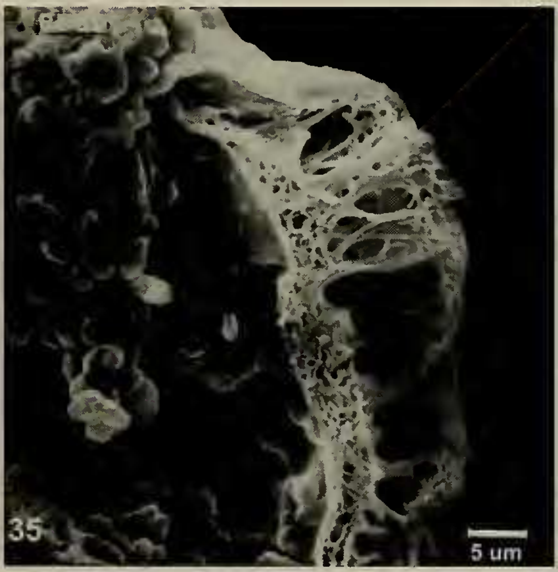
Figure 25. *Branchinella arborea* cyst ridge. Bar = 5 µm.
Figure 26. *Branchinella arborea* cyst shell cross section. Bar = 5 µm.
Figure 27. *Branchinella australiensis* cyst. Bar = 20 µm.
Figure 28. *Branchinella australiensis* cyst ridge structure. Bar = 5 µm.
Figure 29. *Branchinella australiensis* cyst shell cross section. Bar = 10 µm.
Figure 30. *Branchinella basipina* cyst. Bar = 50 µm.











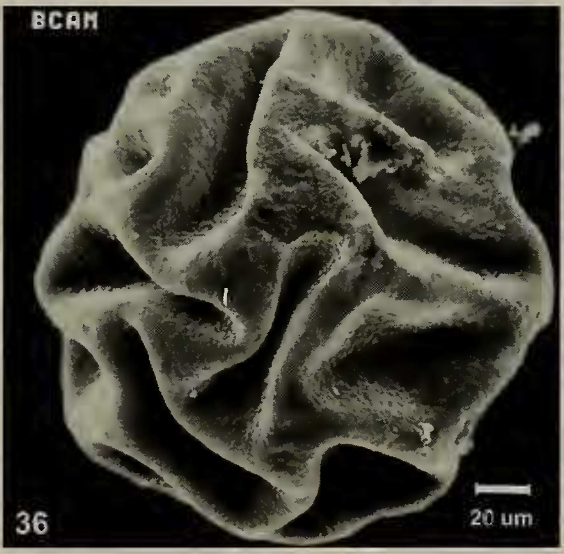
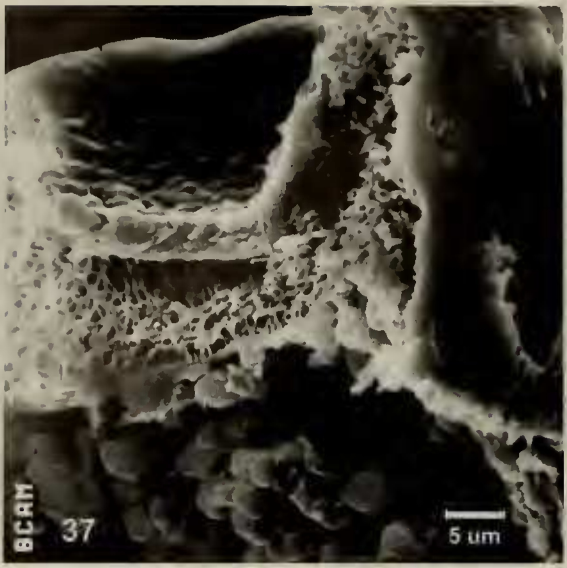
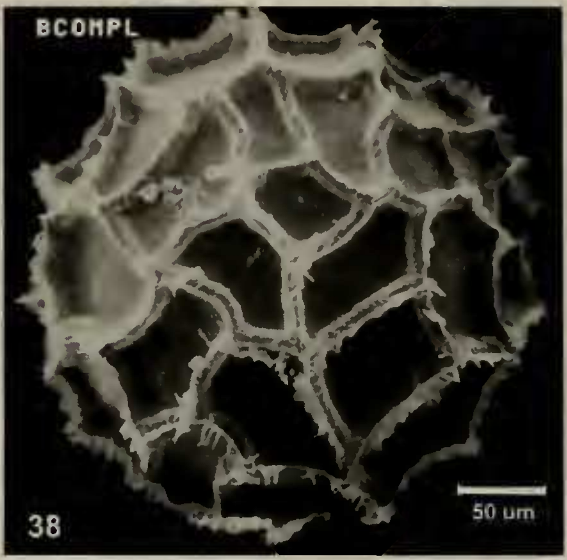
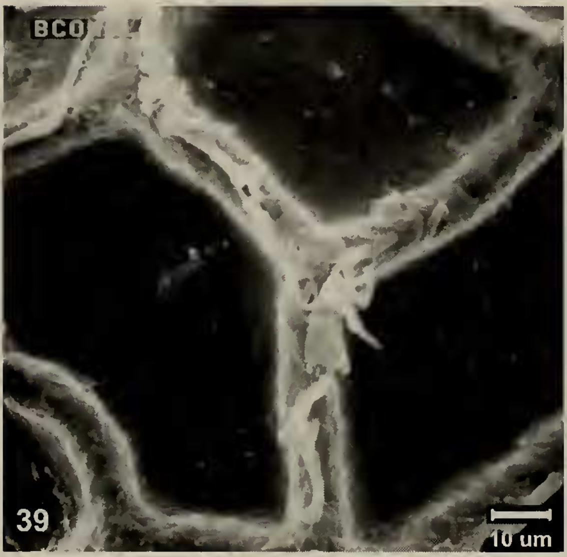
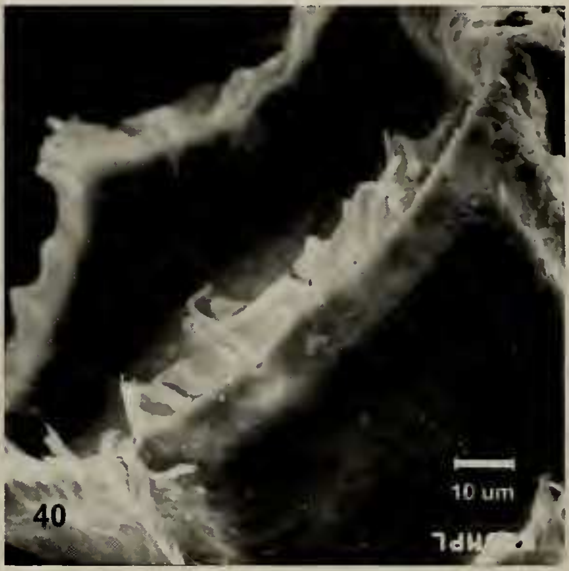


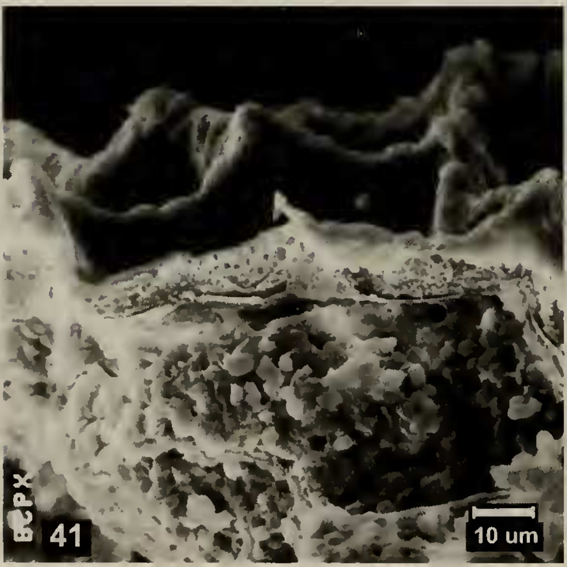
Figure 31. *Branchinella basipina* cyst shell cross section. Bar = 10 µm.
Figure 32. *Branchinella buchananensis* cyst. Bar = 50 µm.
Figure 33. *Branchinella buchananensis* cyst shell cross section. Bar = 10 µm.
Figure 34. *Branchinella budjiti* cyst. Bar = 20 µm.
Figure 35. *Branchinella budjiti* cyst shell cross section. Bar = 5 µm.
Figure 36. *Branchinella campbelli* cyst. Bar = 20 µm.











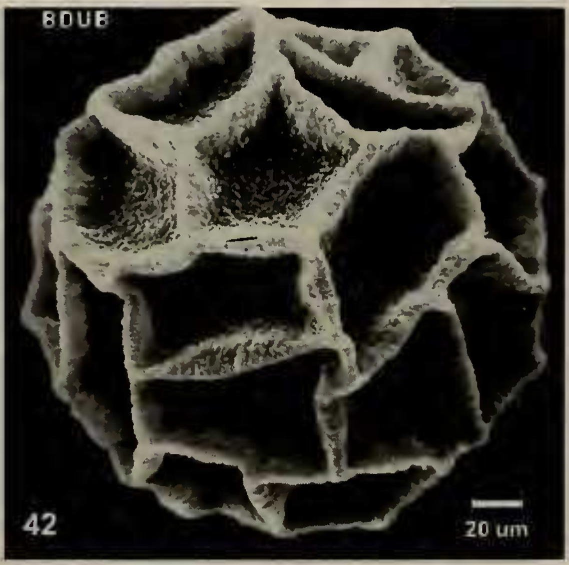
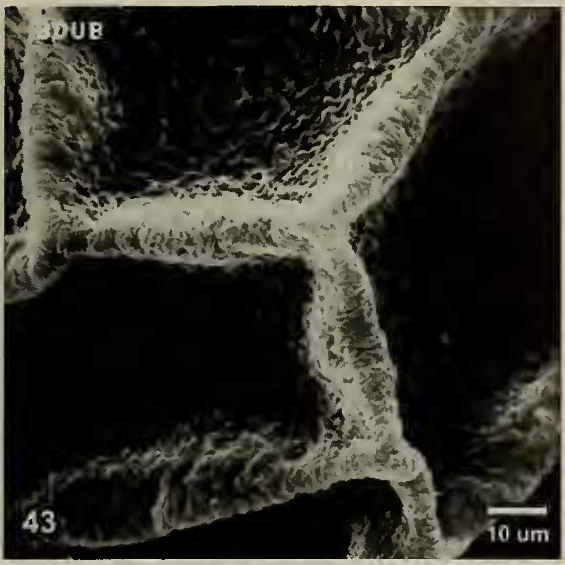
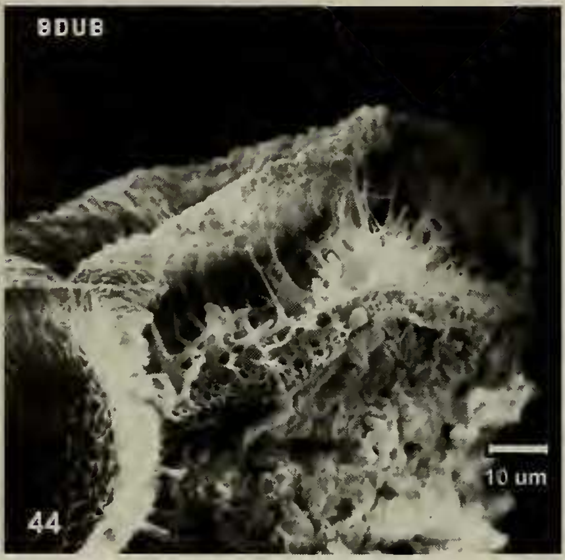
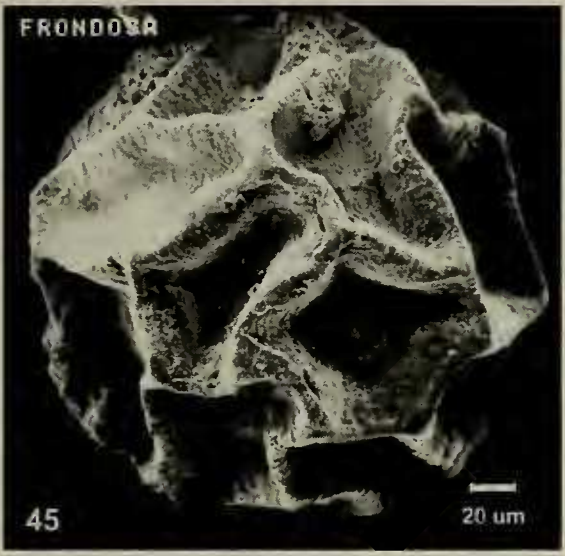
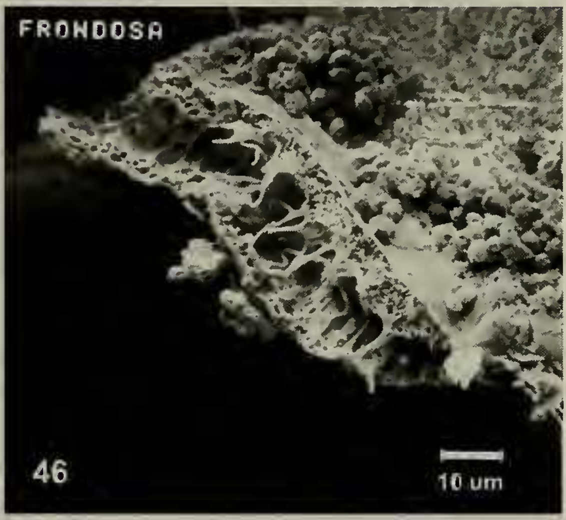


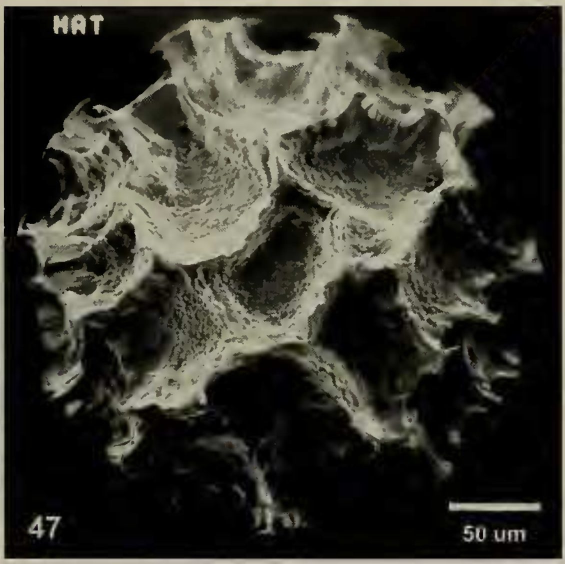
Figure 37. *Branchinella campbelli* cyst shell cross section. Bar = 5 µm.
Figure 38. *Branchinella complexidigitata* cyst. Bar = 50 µm.
Figure 39. *Branchinella complexidigitata* cyst surface structure. Bar = 10 µm.
Figure 40. *Branchinella complexidigitata* cyst surface structure. Bar = 10 µm.
Figure 41. *Branchinella complexidigitata* cyst shell cross section. Bar = 10 µm.
Figure 42. *Branchinella dubia* cyst. Bar = 20 µm.











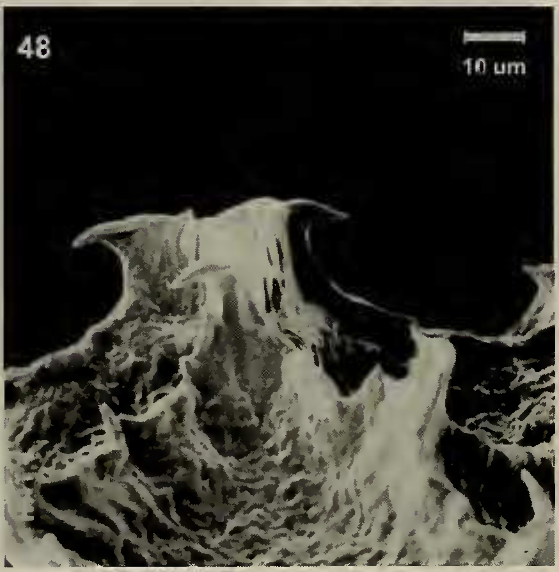
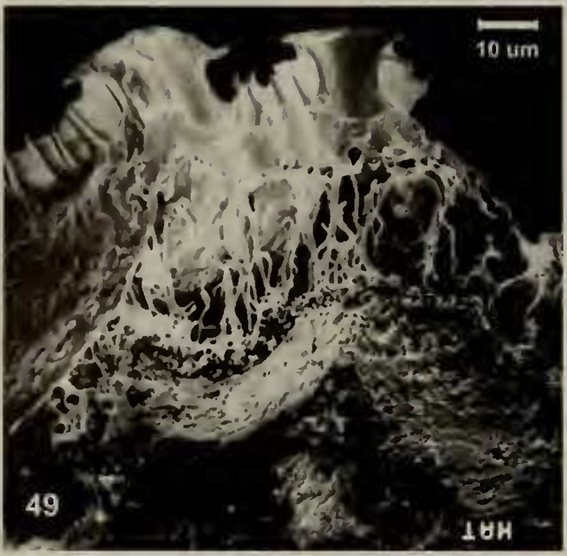
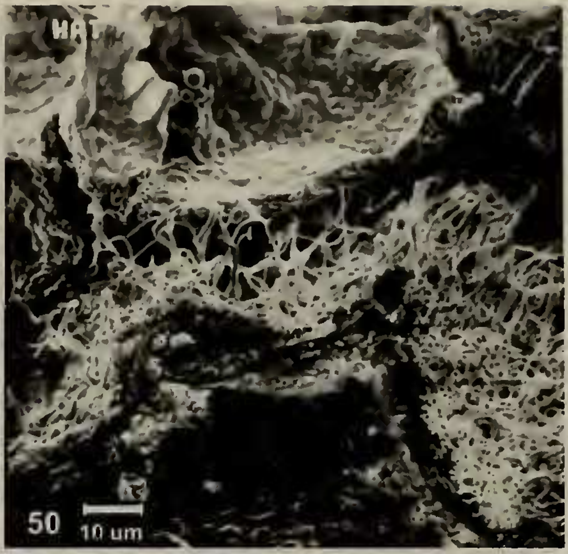
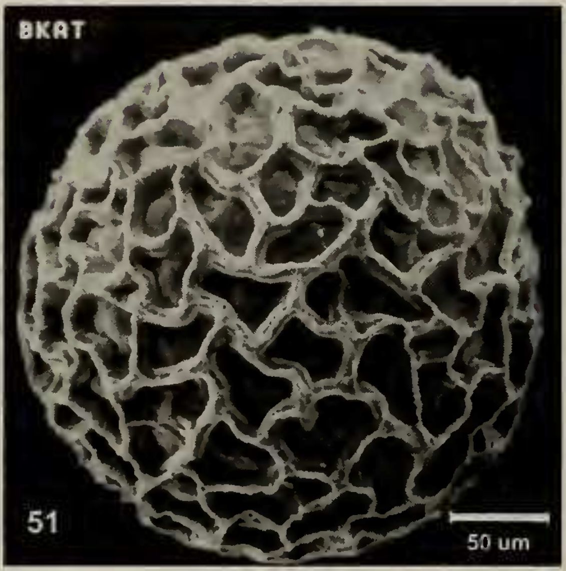
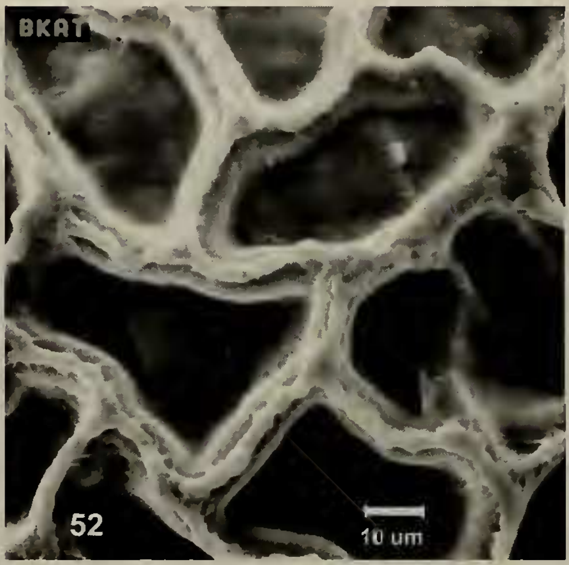


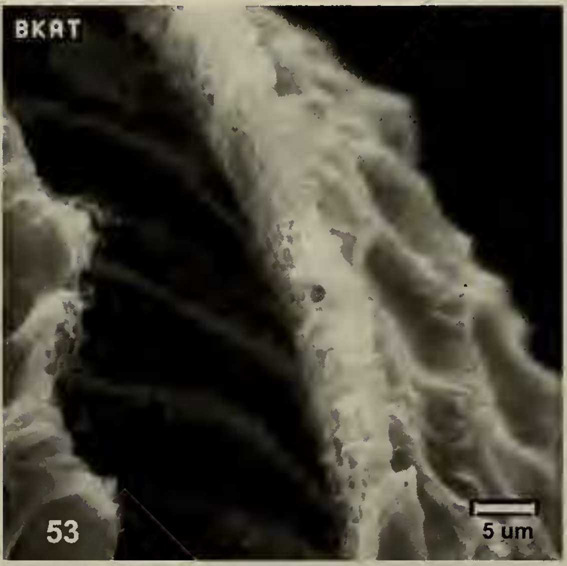
Figure 43. *Branchinella dubia* cyst surface. Bar = 10 μm.
Figure 44. *Branchinella dubia* cyst shell cross section. Bar = 10 μm.
Figure 45. *Branchinella frondosa* cyst. Bar = 20 μm.
Figure 46. *Branchinella frondosa* cyst shell cross section. Bar = 10 μm.
Figure 47. *Branchinella hattahensis* cyst. Bar = 50 μm.
Figure 48. *Branchinella hattahensis* cyst surface structure. Bar = 10 μm.











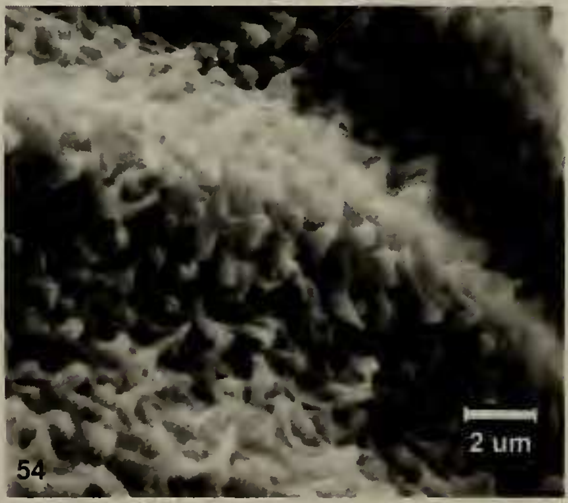
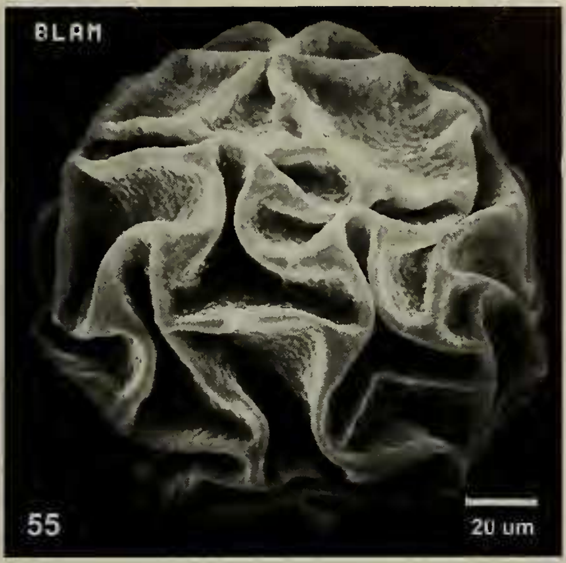
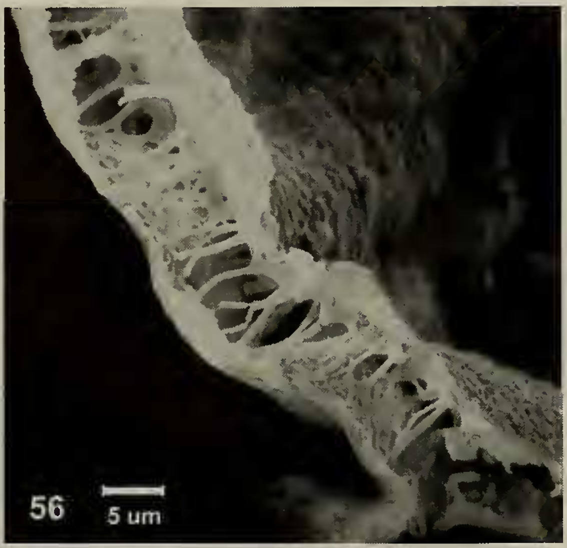
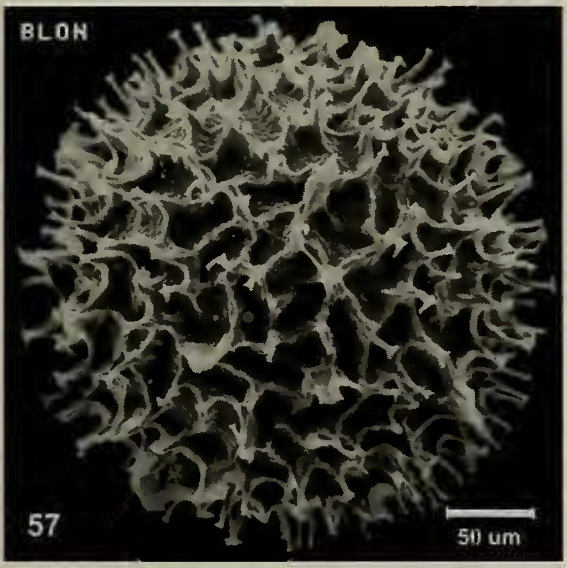
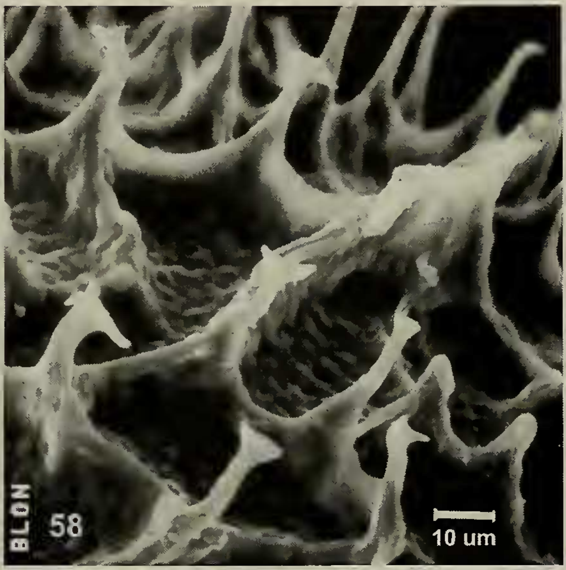


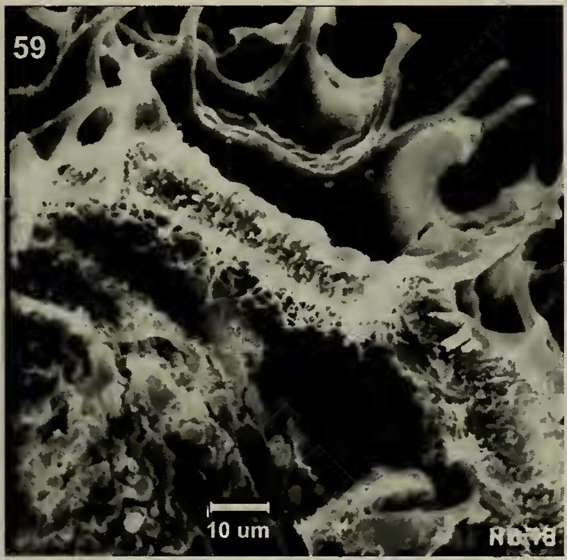
Figure 49. *Branchinella hattahensis* cyst shell cross section with ridge spines. Bar = 10 μm.
Figure 50. *Branchinella hattahensis* cyst shell cross section. Bar = 10 μm.
Figure 51. *Branchinella kadjikadji* cyst. Bar = 50 μm.
Figure 52. *Branchinella kadjikadji* cyst surface. Bar = 10 μm.
Figure 53. *Branchinella kadjikadji* cyst shell cross section showing outer sublayer of alveolar layer pulled away from inner sublayer. Bar = 5 μm.
Figure 54. *Branchinella kadjikadji* cyst shell fracture showing inner sublayer of alveolar layer. Bar = 2 μm.











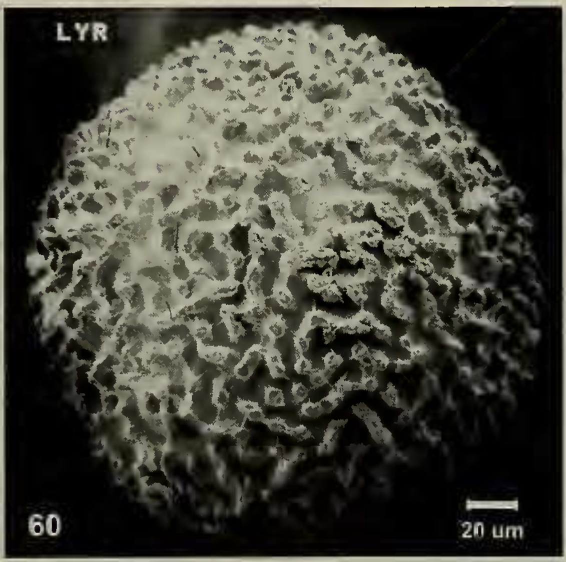
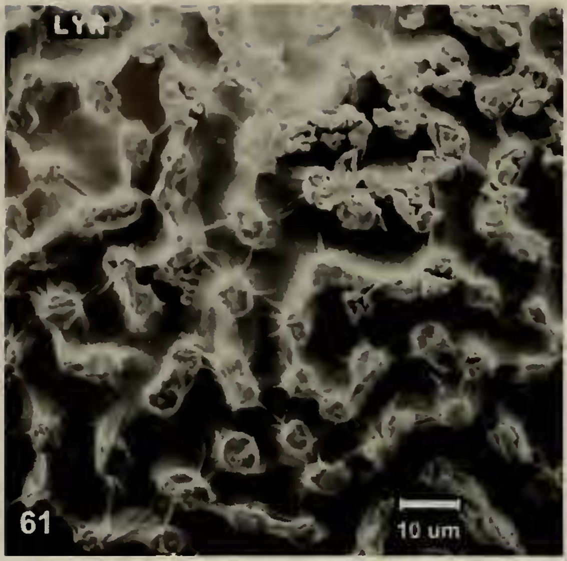
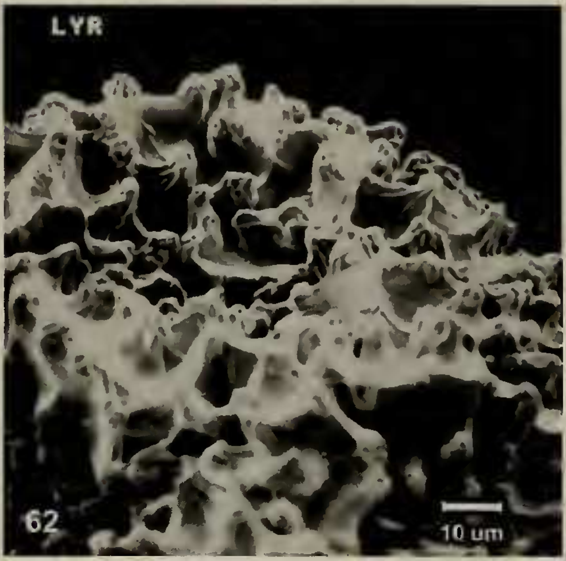
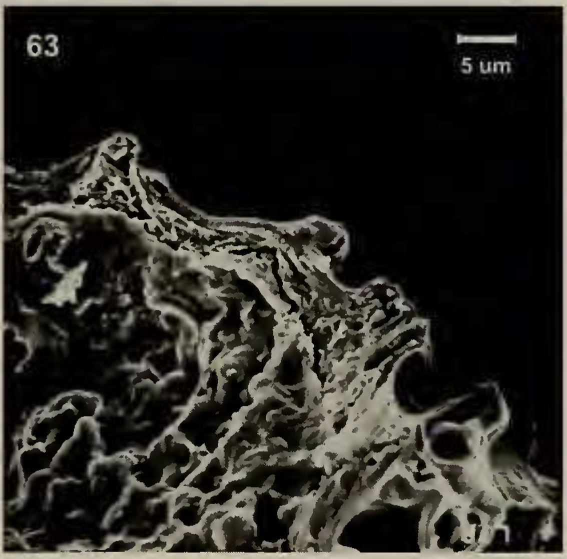
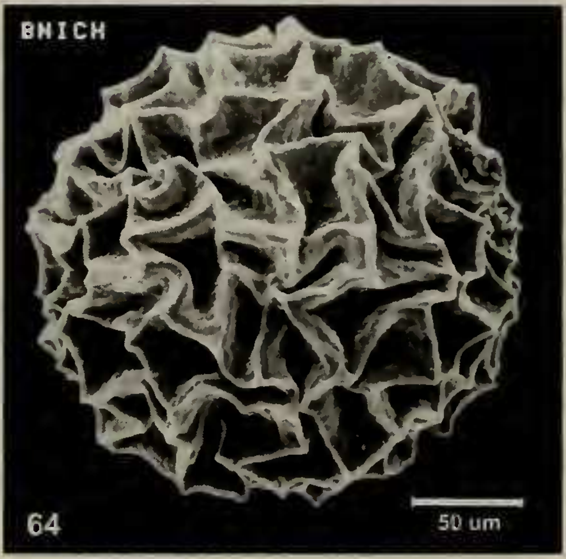


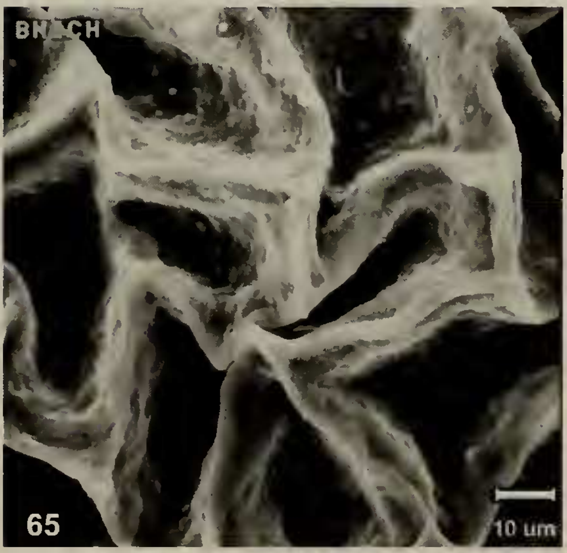
Figure 55. *Branchinella lamellata* cyst. Bar = 20 µm.
Figure 56. *Branchinella lamellata* cyst shell cross section. Bar = 5 µm.
Figure 57. *Branchinella longirostris* cyst. Bar = 50 µm.
Figure 58. *Branchinella longirostris* cyst surface structure. Bar = 10 µm.
Figure 59. *Branchinella longirostris* cyst shell cross section. Bar = 10 µm.
Figure 60. *Branchinella lyrifera* cyst. Bar = 20 µm.











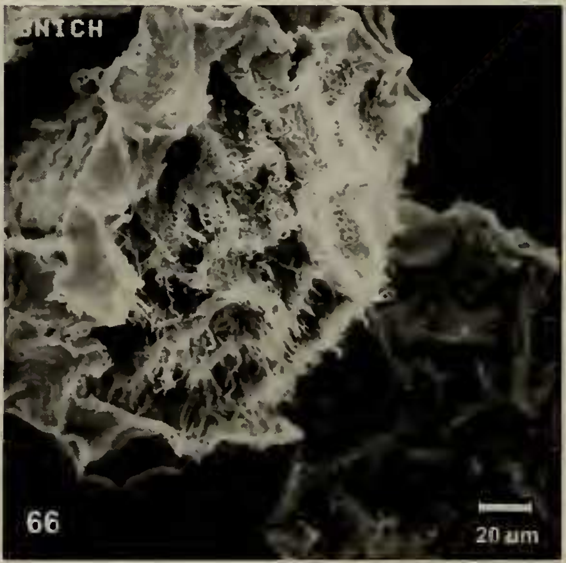
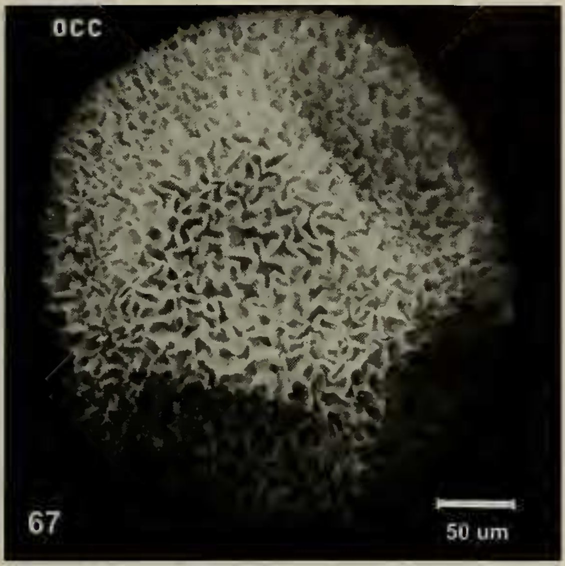
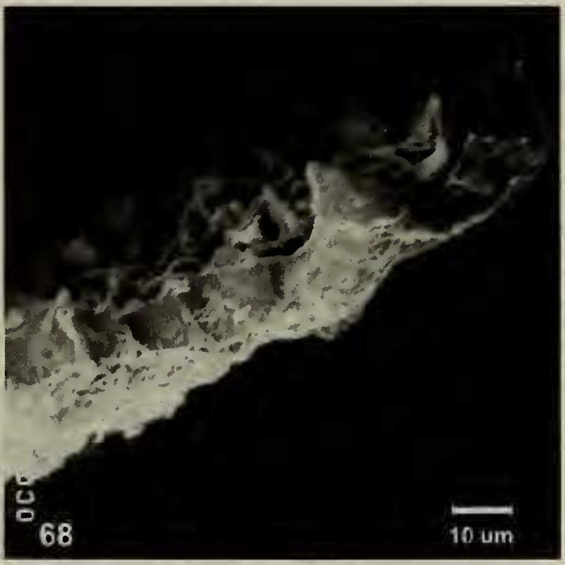
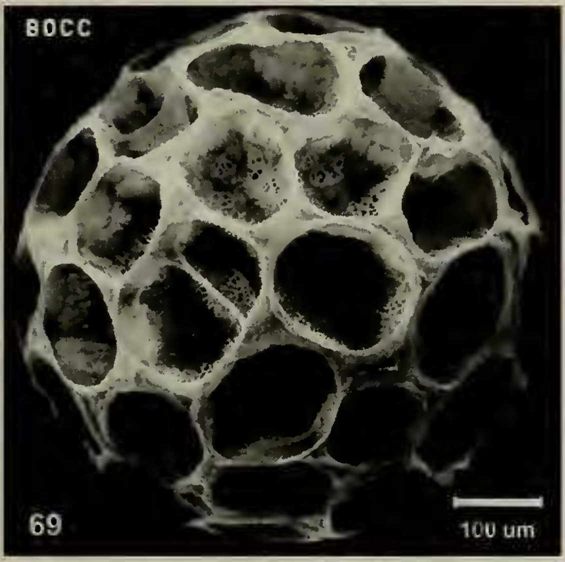
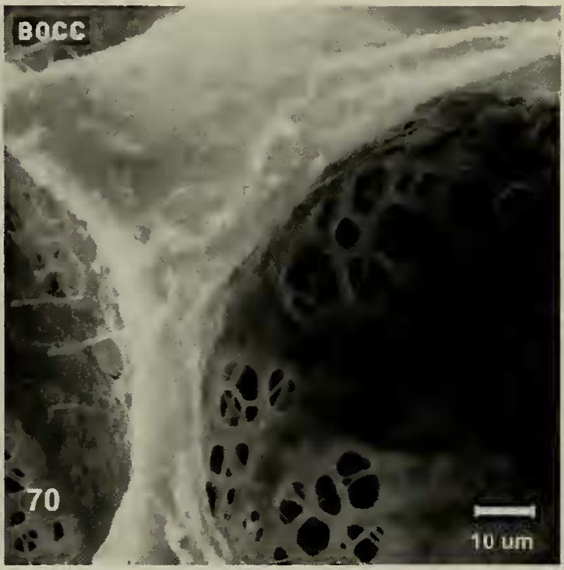


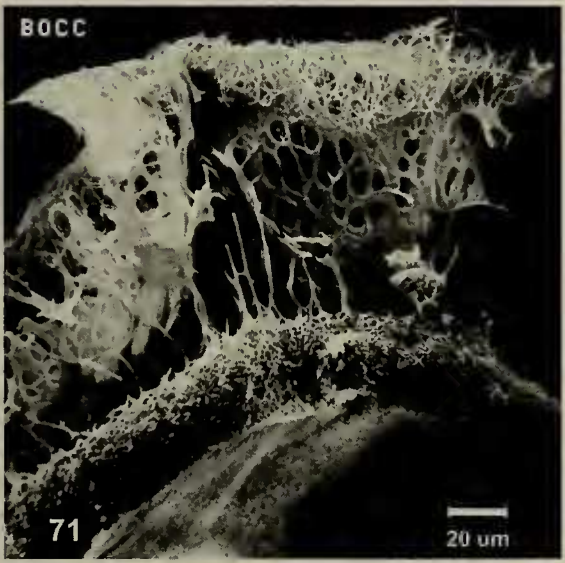
Figure 61. *Branchinella lyrifera* cyst ridges, polar view. Bar = 10 µm.
Figure 62. *Branchinella lyrifera* cyst ridges, side view. Bar = 10 µm.
Figure 63. *Branchinella lyrifera* cyst shell cross section. Bar = 5 µm.
Figure 64. *Branchinella nichollsi* cyst. Bar = 50 µm.
Figure 65. *Branchinella nichollsi* cyst ridge. Bar = 10 µm.
Figure 66. *Branchinella nichollsi* cyst shell cross section. Bar = 20 µm.











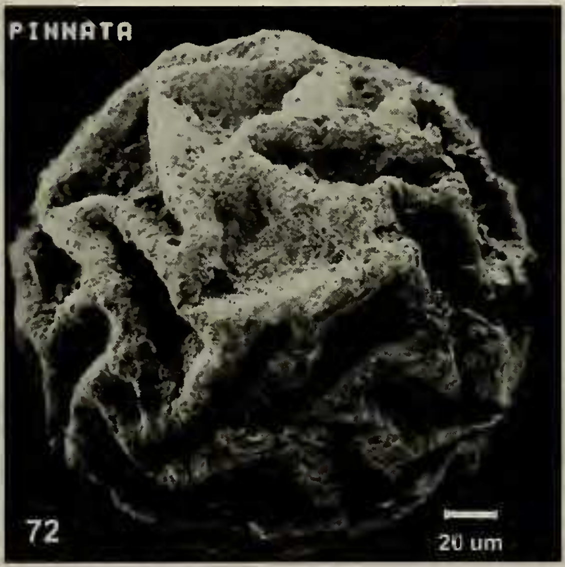
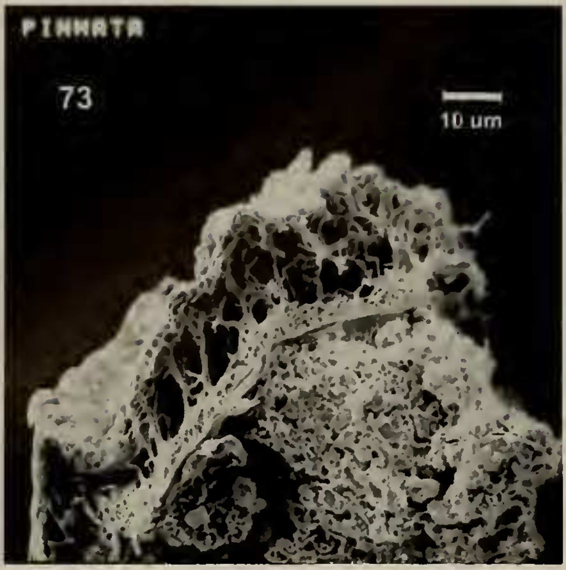
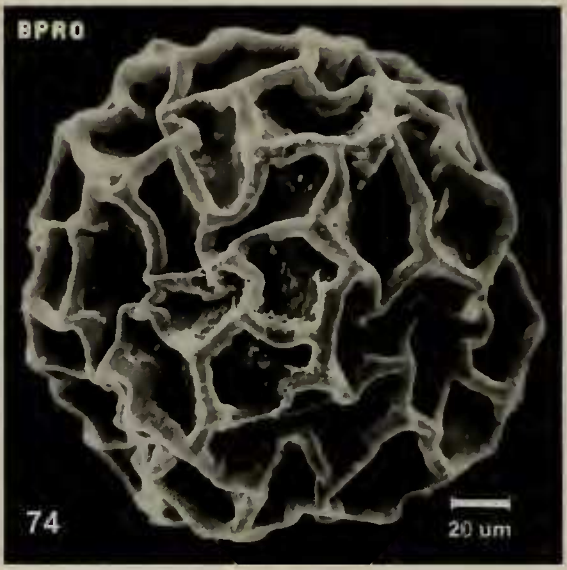
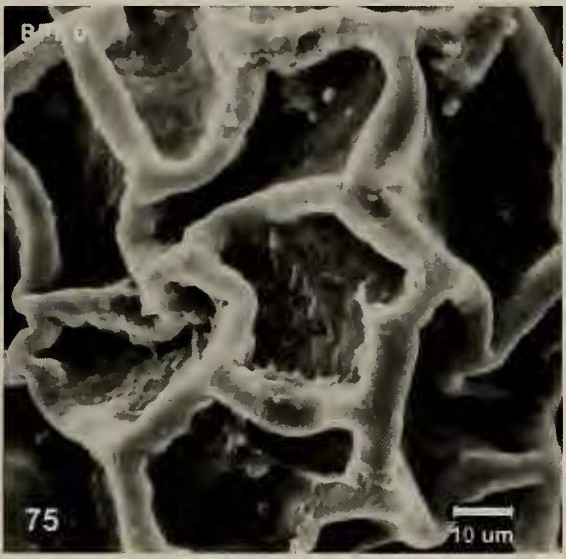
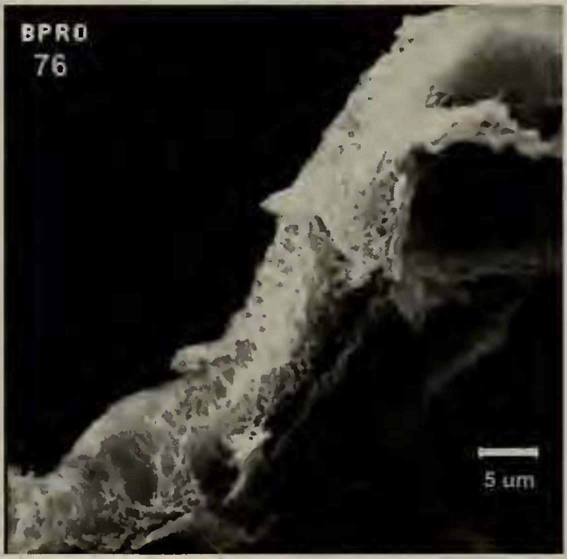


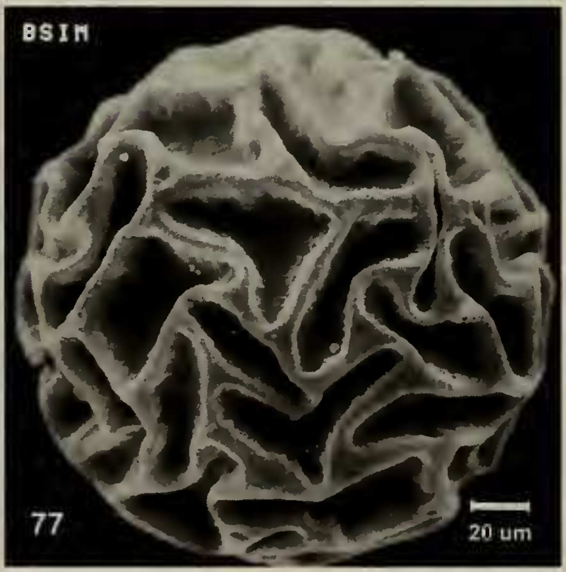
Figure 67. *Branchinella occidentalis* cyst (type I). Bar = 50 μm.
Figure 68. *Branchinella occidentalis* cyst (type I) shell cross section. Bar = 10 μm.
Figure 69. *Branchinella occidentalis* cyst (type II). Bar = 100 μm.
Figure 70. *Branchinella occidentalis* cyst (type II) surface. Bar = 10 μm.
Figure 71. *Branchinella occidentalis* cyst (type II) shell cross section. Bar = 20 μm.
Figure 72. *Branchinella pinnata* cyst. Bar = 20 μm.











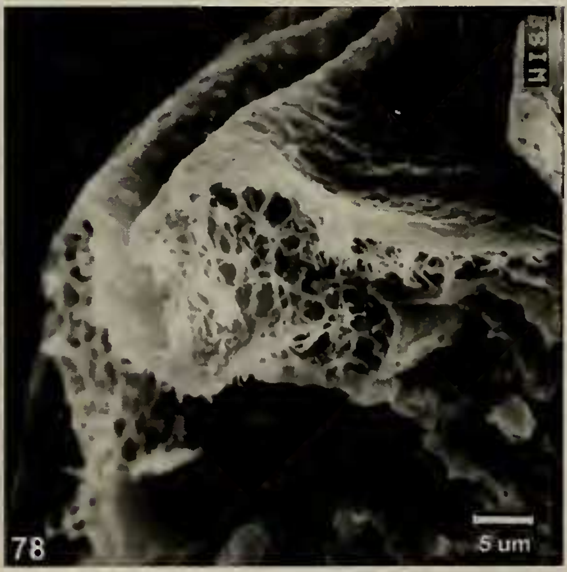
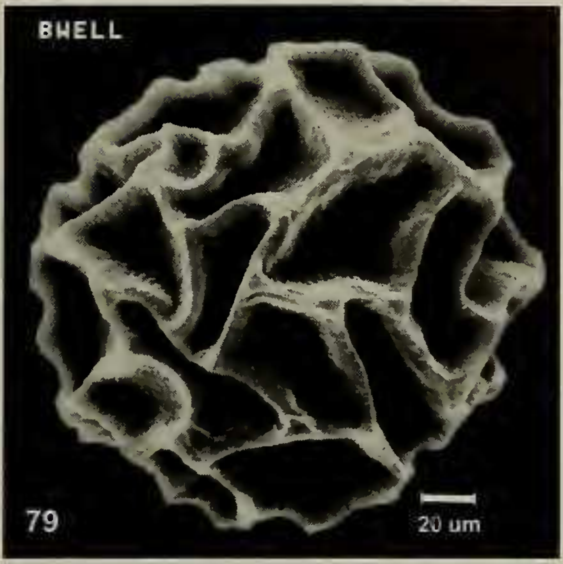
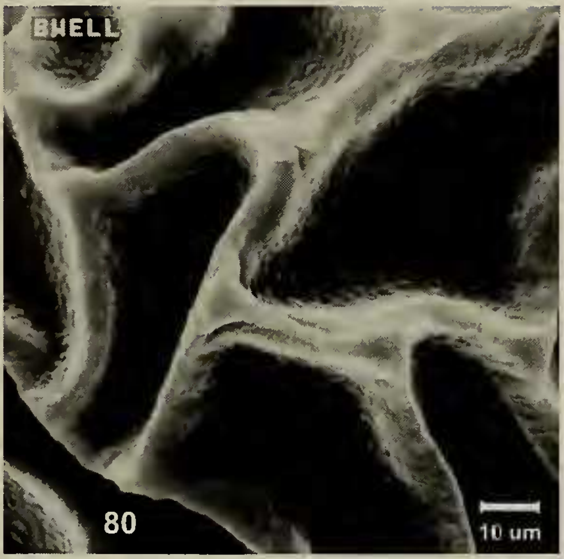


Figure 73. *Branchinella pinnata* cyst shell cross section. Bar = 10 μm.
Figure 74. *Branchinella probiscida* cyst. Bar = 20 μm.
Figure 75. *Branchinella probiscida* cyst surface. Bar = 10 μm.
Figure 76. *Branchinella probiscida* cyst shell cross section. Bar = 5 μm.
Figure 77. *Branchinella simplex* cyst. Bar = 20 μm.
Figure 78. *Branchinella simplex* cyst shell cross section. Bar = 5 μm.





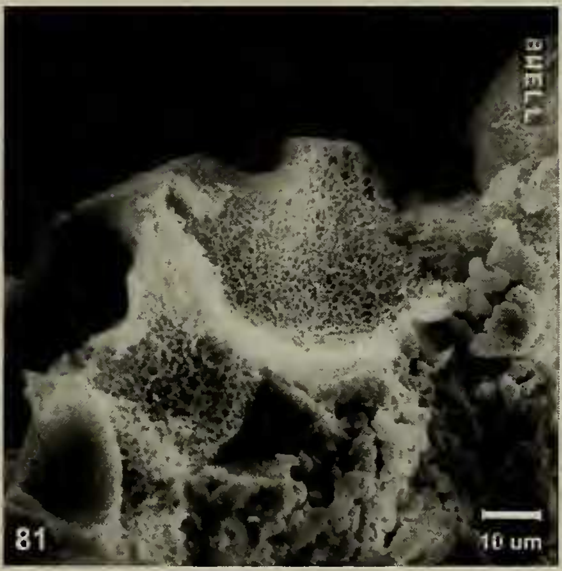


Figure 79. *Branchinella wellardi* cyst. Bar = 20 µm.
Figure 80. *Branchinella wellardi* cyst ridges. Bar = 10 µm.
Figure 81. *Branchinella wellardi* cyst shell cross section. Bar = 10 µm.